

VARIATION AMONG FREE-LIVING SPOTTED HYENAS
IN THREE PERSONALITY TRAITS

By

Kathryn Cushing Shaw

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ABSTRACT

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Inter-individual differences in behavior, termed “animal personality,” are often consistent over time and across contexts, and can be significantly related to fitness. Most studies of animal personality are conducted in the laboratory on captive animals or with experimental protocols on wild animals; few studies have used observational data from free-living animals to examine personality. In this dissertation, I use longitudinal data collected under naturalistic conditions to study personality in a wild population of spotted hyenas (*Crocuta crocuta*). This study is the first to examine the stability, the proximate causes, and the fitness implications of consistent inter-individual differences in a large, free-living carnivore.

I investigated three personality traits that are particularly pertinent to survival and reproduction in spotted hyenas: boldness, aggressiveness, and sociability. Lions are a major source of mortality for hyenas, yet hyenas regularly interact with them directly due to the potential benefits of acquiring food. Because hyenas must balance the risk of injury or death with the benefits of resource acquisition, lion-hyena interactions offer a promising way to study boldness. Aggression is frequent and easily observable in hyenas; moreover, it is tightly coupled with access to food, which is a major determinant of reproductive success in this species. Finally, hyenas vary in their propensity to engage in social behavior with conspecifics,

and sociability has been shown to affect fitness in species with societies that are remarkably similar in size and structure to those of spotted hyenas.

I found significant differences among individual hyenas in all three traits. However, whereas both sexes exhibited consistent inter-individual differences in aggressiveness and sociability, males were less consistent than females in their boldness; this may be due to their low social status and reduced access to resources. Attributes of the individual (e.g. social rank) and situational factors (e.g. seasonal prey availability) affected all three personality traits.

Heritability and maternal effects were significant, but small, for both boldness and sociability. A much larger proportion of the variation in aggressiveness could be attributed to genetic and maternal effects, supporting previous research linking hormone exposure in utero to aggressive behavior later in life. Whereas both boldness and aggressiveness were stable across age classes, sociability changed across ontogeny and the nature of this change varied with social rank. The advantages of associating with dominant hyenas, such as increased feeding tolerance, may be especially important for low-ranking individuals. Interestingly, the fitness benefits of sociability and aggression also varied with rank; high rates of aggression and sociability enhanced the reproductive success of low-ranking hyenas more than that of high-ranking hyenas. For low-ranking hyenas, gaining feeding tolerance via sociability or increasing resource-holding potential via aggressiveness may significantly enhance reproductive success.

Both boldness and sociability were linked to survival, but these traits affected longevity in different ways. Highly social hyenas lived longer than those that were less social; meanwhile, selection on boldness was stabilizing, favoring hyenas with intermediate boldness values that struck a balance between the benefits of risky behavior and the risks of injury and death.

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CHAPTER 1

GENERAL INTRODUCTION

Understanding animal behavior has been a major component of biological research for centuries; naturalists and scientists have long been interested in how and why animals behave the way they do (e.g. Darwin 1872; Aristotle 1929; Hinde 1970). Until recently, much of the focus of behavioral research on non-human animals has been at the level of species, rather than at the level of the individual (Jolly 1966; Geist 1974; Yasukawa & Searcy 1982; Thierry 1985). However, in recent years researchers have begun to document significant differences in behavior among individuals within a single population (e.g. Wilson et al. 1994; Reale et al. 2000; Dall et al. 2004; Carere & Eens 2005). Moreover, these differences are often consistent over time and across contexts, and can have significant implications for fitness (Duckworth 2006; Johnson & Sih 2007; Silk et al. 2010; Vainikka et al. 2010). This type of variation has been referred to as “individual differences,” “temperament,” “coping styles,” “behavioral syndromes,” and “animal personality” (e.g. Macdonald 1983; Capitanio 1999; Koolhaas et al. 1999; Reale & Festa-Bianchet 2003; Johnson & Sih 2005).

Evidence for personality has been found in species as diverse as squid, sunfish, great tits, marmots, and chimpanzees (Armitage 1986a; Coleman & Wilson 1998; Dingemanse et al. 2003; Sinn & Moltschaniwskyj 2005; Anestis et al. 2006). The literature on personality in humans and their companion animals is also extensive (e.g. Eysenck 1953; Wilsson & Sundgren 1997; Ebstein et al. 2002). In most species in which personality has been studied, individuals tend to vary across similar dimensions, such as aggressiveness, boldness, activity, sociability,

and exploration (for reviews, see Sih et al. 2004, Reale et al. 2007). However, in species where consistent individual differences have been found, males and females may differ in repeatability. For instance, male guppies are less consistent in their boldness than are female guppies (Harris et al. 2010), yet theory predicts that males should be more consistent in aggressive behavior than females due to high testosterone levels (Wingfield 1994). In a meta-analysis, Bell et al. (2009) found that differences between males and females in behavioral repeatability vary based on the species and the traits being studied; this suggests that, in terms of consistency, the optimal strategy for each sex may be determined separately in each species based on specific aspects of its environment, life history, and morphology.

One important question addressed by personality research is how stable traits are, both over time and across different contexts. For instance, whereas Sinn et al. (2008) found that juvenile boldness predicted adult boldness in squid, studies in other species suggest that personality may change across ontogeny via experience, physiological development, or changing environmental conditions (Bell & Stamps 2004; Dingemanse et al. 2009; Stamps & Groothuis 2010). There is also great debate as to the effect of context on personality; for instance, are individuals that are aggressive in one context also aggressive in another (i.e. domain-general), or is aggressiveness in different contexts unrelated (i.e. context-specific)? Some studies have suggested that personality traits in humans and other animals are context-specific (Kagan 2003; Sinn & Moltschaniwskyj 2005; Tanner & Adler 2009), but there are also several well-established examples of domain-generality in personality (e.g. Johnson & Sih 2007).

Artificial selection for personality traits has been very successful; researchers have been able to breed strains of very social mice and highly exploratory great tits (Carere et al. 2005; Sankoorikal et al. 2006), suggesting that heritability plays a significant role in some personality traits. A heritability estimate is the proportion of the observed phenotypic variance in a trait that can be explained by genetics; heritability has been estimated to be as high as 0.61 for aggression in vervet monkeys (Fairbanks et al. 2004) and 0.89 for reactivity in dumpling squid (Sinn et al. 2006). However, not all traits appear to be equally heritable in all species; for instance, less than one percent of the variation in aggressiveness observed in a population of sticklebacks could be explained by genetics (Bell 2005).

Another major focus of research on animal personality in recent years has been the relationship between fitness and inter-individual differences in behavior. Many studies suggest that personality has significant implications for reproductive success and survival. Among some primates, females with strong social ties to other group members have greater longevity than less social females (Silk et al. 2010). However, extreme trait values may also have negatively correlated with fitness; Packer et al. (1995) found that aggressive, high-ranking female baboons had reduced fertility and a higher incidence of miscarriages than did less dominant females. In other species, the consequences of personality may vary with fluctuating environmental conditions. For instance, in bighorn sheep, shy females suffer higher mortality than do bold females in years when predation pressure is high, but not in years of reduced predation (Reale & Festa-Bianchet 2003).

Here, I present a study of personality in the spotted hyena (*Crocuta crocuta*). Since 1988, the Mara Hyena Project has continuously observed a group of free-living hyenas in the

Masai Mara National Reserve in Kenya. Collaborators on this project have collected a variety of behavioral, demographic, morphological, genetic, and physiological data on these hyenas. This rich longitudinal dataset has enabled me to examine the heritability, stability, and fitness consequences of behavioral traits under naturalistic conditions. To date, personality has most often been examined in captive individuals in the laboratory, or with experimental protocols on wild animals (Armitage 1986a; Wilson et al. 1993; Brown et al. 2007; Fox et al. 2009; Taylor et al. 2012). However, Wilson et al. (1994) suggest that the behavior of an individual in the laboratory may not accurately reflect its behavior in the wild. Whereas lab-based and experimental studies have the advantage of enhanced control, direct observational data documenting personality traits under strictly natural conditions offers a means to assess simultaneously how such traits vary among free-living individuals, and how they affect fitness. Only a small number of studies to date have been able to assess personality with the naturally-occurring behavior of free-living animals (e.g. Armitage 1986b; McPhee & Quinn 1998; Silk et al. 2010).

In this dissertation, I examine three personality traits in spotted hyenas: boldness, aggressiveness, and sociability. These traits are all characterized by frequent and easily observable behavior in this species, and each has direct implications for fitness. Other personality traits that have been identified in various species, such as activity and docility, are worthy of future study, but their potential consequences for survival and reproduction in hyenas are less clear.

Boldness is a particularly important personality trait to understand, because predation is one of the most significant selection pressures in determining behavior (Lima & Dill 1990; Lima

1998). Although lions are a major source of hyena mortality, hyenas do not actively avoid lions (Watts & Holekamp 2009). Unlike most other species, hyenas have significant incentives to interact directly with their predators; they are able to steal food from lions in some situations, and are often forced to defend their own kills from lions (Kruuk 1972; Mills 1990; Watts & Holekamp 2009). Hyenas therefore face a particularly interesting tradeoff with respect to lions, balancing the risk of injury or death with the potential benefits of acquiring or retaining possession of food. In a larger framework, understanding individual differences in boldness among large carnivores is important in several ways. Shy individuals are prone to being undersampled (Wilson et al. 1994), so it is important to understand in what types of species shy-bold continuums exist, and what sex and age classes are most likely to exhibit consistent differences in boldness. It is also hypothesized that bolder carnivores are more likely to become “problem individuals” that kill livestock and pets (Linnell et al. 1999; Darrow & Shivik 2009). Studies of boldness in large carnivores are necessary to clarify the processes by which individuals become “problems,” and to identify which individuals in each species are particularly prone to livestock and pet depredation.

Aggressiveness among animals is a particularly important trait to understand, since in many species, aggression facilitates access to resources. Consistent inter-individual variation in aggressiveness has been documented in several species, including three-spined sticklebacks (Bakker 1986), red squirrels (Taylor et al. 2012), and vervet monkeys (Fairbanks et al. 2004). However, aggressiveness has not been examined in any species with sex role reversals, where females are socially dominant to, and often more aggressive than, males. In these species, the proximate causes and the fitness consequences of aggressive behavior may be very different

than those in species where males are dominant. Spotted hyena societies are female-dominated, and female hyenas exhibit more frequent and intense aggressive behavior than males do (Kruuk 1972; Van Meter 2009). Among hyenas, aggressive behavior occurs in several contexts, including food-related and non-food related situations; the occurrence of aggressive behavior in these different contexts permits a study of context-specificity in aggression. Additionally, since access to resources drives reproductive success in hyenas (Holekamp & Smale 1996), aggression may be significantly related to fitness in this species.

Whereas sociability has been well-studied in humans and other primates, far fewer studies have examined this personality trait in other taxa. Previous research suggests that sociability is significantly related to fitness; individuals with stronger social bonds and those that engage in social behavior more often tend to have better reproductive success and increased longevity, compared to less social individuals (Silk et al. 2003; Cote et al. 2008; Cameron et al. 2009; Silk et al. 2010; Schulke et al. 2010). Spotted hyenas are highly gregarious and live in large fission-fusion groups, where subgroups change in size and composition on short time scales (Holekamp et al. 2006). These social dynamics, in addition to the frequent affiliative behaviors demonstrated by hyenas, offer a promising way to study inter-individual variation in sociability. Previous research on hyenas has demonstrated significant advantages to engaging in social behavior (Holekamp et al. 1997; Boydston et al. 2001; Smith et al. 2007; Smith et al. 2011), suggesting that sociability may be positively correlated with survival and reproductive success in this species.

Mine is not the first study of inter-individual differences in the behavior of hyenas; Gosling (1998) studied personality in a group of captive spotted hyenas. In this study, observers

who were familiar with the hyenas were asked to rate them on several personality traits. The ratings for many traits, including “affiliative,” “bold,” “aggressive,” “nervous,” and “nurturant,” were highly reliable, with inter-observer reliabilities averaging 0.71. These results suggest that hyenas vary along several behavioral axes, and that these differences can be reliably quantified by different observers. However, the study does have some shortcomings. For instance, the trait ratings were not independent because the polled observers worked together closely, and had likely discussed these hyenas in detail before the polling commenced. Additionally, the hyenas were rated on their past behavior, so it is possible that particularly salient memories affected observers’ ratings. Finally, although Gosling went to great lengths to define each trait, the setup of the study made it impossible to eliminate subjectivity.

Since this early research, other studies have documented inter-individual differences in the behavior of hyenas. Via playback experiments, Watts et al. (2010) determined that individual hyenas varied in the way they responded to lion roars. The authors also found a correlation between boldness and vigilance behavior; hyenas that took more risks than other individuals in response to the playback also tended to be more vigilant than other hyenas. These differences were context-specific, seen only in the context of interactions with lions, not at dens or in situations where lions were absent. Pangle (2008) reported evidence of consistent differences in vigilance behavior among adult hyenas, but not among juveniles. Finally, both Dloniak et al. (2006) and Van Meter (2009) found correlations between circulating maternal fecal androgen levels during gestation and the aggression rates of offspring, suggesting that hormone-mediated maternal effects play a significant role in shaping individual differences in aggressive behavior among hyenas.

While this research has been instrumental in laying the groundwork for personality research in spotted hyenas, no previous study has synthesized genetic, behavioral, and fitness data to understand inter-individual variation in this species in a broader sense. My dissertation work is the first to examine the stability, the proximate causes, and the fitness implications of consistent inter-individual differences in a large, free-living carnivore.

Overview of chapters

Each subsequent chapter in this dissertation is a systematic study of a different personality trait in a group of free-living spotted hyenas. In each chapter, I first investigate the situational and individual variables that contribute to the trait, and determine whether there is evidence of consistent inter-individual differences in the trait. Then, I determine whether genetics or maternal effects contribute significantly to phenotypic variation in the trait, and whether the trait is stable across ontogeny. Finally, I assess whether there is a relationship between the trait and various measures of fitness.

In Chapter Two, I investigate boldness in hyenas, using the distances maintained between hyenas and lions as a measure of boldness. I found that, whereas female hyenas exhibited consistent inter-individual differences in boldness, males were more plastic in their behavior around lions. Although this bears further research, sex differences in plasticity may be related to social rank and access to resources in this species. Situational variables were very important in determining how closely hyenas approached lions, and genetic and maternal effects only played a small role in boldness. Boldness in juveniles was a good predictor of boldness during adulthood, indicating that for hyenas, this trait is determined relatively early in

life. Although I found no correlation between boldness and reproductive success, I did find that it was significantly related to longevity; hyenas with particularly low and high boldness measures died at younger ages than did those with intermediate boldness values. Whereas the boldest animals may be especially prone to injury and death due to their propensity to take life-threatening risks, the shyest animals may fail to reap the benefits of risky behavior.

In the third chapter, I study the frequency and intensity of aggressive behavior in two contexts: food-related aggressions and non-food-related aggressions. Both males and females showed consistent inter-individual differences in the intensity of aggression, but hyenas were not consistent across repeated observations in the frequency of either type of aggression. However, when averaged over the lifetime of individuals, there were clear differences among hyenas in both food-related and non-food-related aggressive behavior. These differences were highly heritable and subject to large maternal effects, echoing previous research indicating that hormone exposure in utero influences the aggressive behavior of hyenas later in life (Dloniak et al. 2006; Van Meter 2009). This early determination of aggressive behavior is also supported by my finding that the intensity of aggressive behavior early in life predicts aggressive behavior during adulthood. Interestingly, aggressive behavior appears to be context-specific; hyenas that emitted high-intensity aggressive acts over food did not necessarily emit high-intensity aggressive acts in other contexts, suggesting different functions, and mediating mechanisms for, different types of aggressive behavior. Whereas aggressiveness in some species decreases some aspects of fitness (e.g. Packer et al. 1995), aggressiveness in hyenas is related to enhanced reproductive success. I found that both food-related and non-food related aggressiveness are positively correlated with reproductive success, although the relationship

between food-related aggressiveness and reproductive success depended on maternal rank. I also found that the offspring of females with high food-related aggression rates were able to feed longer at kills among conspecifics than the offspring of mothers that aggressed less frequently over food. Because access to resources drives variation in reproductive success in female hyenas (Holekamp & Smale 1996), aggressiveness may benefit females and their offspring by allowing them to more successfully monopolize food resources.

In Chapter Four I investigate sociability, using several different trait measures such as the frequency at which hyenas solicit greetings and the rate at which they join subgroups. Both males and females were consistent in their greeting behavior across repeated observations. Greeting rate and joining rate were both significantly heritable, but only a small portion of the variation in each of these behaviors could be explained by maternal effects. Interestingly, whereas I found in previous chapters that both boldness and aggressiveness are stable across ontogeny, sociability changes in different ways across age classes in various individuals. Changes in sociability across ontogeny depend on social rank; as they reach reproductive maturity, low-ranking hyenas, but not high-ranking hyenas, tend to increase in their tendency to solicit greetings. The advantages of associating with dominant hyenas, such as increased feeding tolerance (Smith et al. 2007), may be especially important for low-ranking hyenas. Although social rank is the major driver of reproductive success among hyenas (Holekamp & Smale 1996; Swanson et al. 2011), inter-individual differences in sociability also contribute to variation in reproductive success. I found that the rate at which females joined groups was positively correlated with various fitness measures, and the benefits for reproductive success were especially strong among low-ranking hyenas. Sociability has similar fitness benefits in

other species (e.g. Silk et al. 2003; Silk et al. 2010), and these positive correlations may be due to advantages conferred by strong cooperative and coalitionary partnerships (Smith et al. 2007).

The research in this dissertation was made possible by collaboration, both in terms of data collection over the last two decades, and also in support provided to me more recently. Because these chapters were prepared in manuscript form and this project was a work of collaboration, I use first person plural in the remainder of this dissertation rather than first person singular.

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CHAPTER 2

INDIVIDUAL DIFFERENCES IN BOLDNESS AMONG SPOTTED HYENAS

INTRODUCTION

In recent years, there has been accumulating evidence of consistent differences in behavior among individuals of a single species, or “animal personality.” Studies have found that many traits, including aggressiveness, activity, boldness, sociability, and exploratory behavior, are consistent over time and across contexts in some species (see Sih et al. 2004 and Reale et al. 2007 for comprehensive reviews). Although it has received considerable attention (e.g. Wilson et al. 1994; Brown et al. 2007; Frost et al. 2007; Chapman et al. 2011), boldness has been one of the more complicated personality traits to study, and it has also proven difficult to understand its implications, due to the difficulties inherent in studying this trait and its consequences under naturalistic conditions.

Riesch et al. (2009) define the boldness of an individual as “the extent to which it is willing to trade off potentially increased predation risks for possible gains in resources.” Because of its direct effects on fitness, predation is one of the most important selection pressures determining behavior (Lima & Dill 1990; Lima 1998). The tremendous significance of predation suggests that boldness may be one of the most important traits to understand, both in terms of how variation in boldness arises and how this variation affects fitness. Boldness has been studied in a variety of species, including fishing spiders (Johnson & Sih 2005), dumpling squid (Sinn et al. 2006), sand fiddler crabs (Pratt et al. 2005), several species of fish (Wilson et al. 1993; Coleman & Wilson 1998; Bell & Stamps 2004; Biro et al. 2009), crayfish (Vainikka et al.

2010), great tits (Carere & van Oers 2004), red squirrels (Boon et al. 2008), kangaroo rats (Dochtermann & Jenkins 2007), and bighorn sheep (Reale et al. 2009). However, whereas these animals all have multiple predators, individual variation in boldness has never been systematically studied in species that experience very little risk of predation in nature, such as large mammalian carnivores. Variation in boldness, as well as the fitness consequences of these differences, may be very different in predator than prey species. Here we evaluate boldness in the second-largest carnivore in Africa, the spotted hyena (*Crocuta crocuta*), for which lions are the only natural predators.

Most, but not all, studies have found boldness to be consistent within individuals and repeatable over time (Johnson & Sih 2005; López et al. 2005; Sinn & Moltschaniwskyj 2005; Niemelä et al. 2012). However, consistent inter-individual differences are not necessarily observable in all subsets of a population. For example, Harris et al. (2010) found that boldness in guppies was repeatable in females but not males, and research by Hedrick and Kortet (2012) showed the same trend in field crickets. Dzieweczynski and Crovo (2011) showed that some, but not all, measures of boldness are repeatable in juvenile sticklebacks.

With few exceptions (e.g. Riesch et al. 2009), most previous studies have found that boldness is significantly heritable, with heritability estimates ranging from 0.002 (Bell 2005) to more than 0.5 (Drent et al. 2003). To date, very few studies have estimated maternal effects on boldness. Reale et al. (2009) found no evidence of maternal effects on boldness in bighorn sheep, and the maternal effect estimate in a study of boldness in great tits was significant, but small, at 0.05 (van Oers et al. 2004).

Findings are inconsistent regarding the stability of boldness over time, particularly before and after the onset of sexual maturity. Magnhagen and Borcharding (2008) found that boldness in perch was age-specific; individuals that were particularly bold as juveniles were not necessarily bold as adults. However, Sinn et al. (2008) found a positive association between feeding-related boldness among individual squid as juveniles and adults, suggesting that phenotypic boldness is determined well before adulthood.

In terms of fitness, theoretical analyses by Wolf et al. (2007) suggest that bolder animals may have shorter lifespans and may invest more in current, rather than future, reproduction. A meta-analysis by Smith and Blumstein (2008) supported this theory, finding that boldness decreased longevity but increased reproductive success in captive animals. Reale et al. (2009) tested this tradeoff with a population of male bighorn sheep and found that bolder rams actually survived longer than shy rams, and that bolder rams also had greater reproductive success later in life than did shy rams. Variation in the relationships between boldness and fitness may be due to species-level differences and exposure to varying intensities of predation pressure.

Most studies of boldness are either performed in the laboratory or use an experimental setup to quantify boldness in a free-living population; novel object tests (e.g. Wilson et al. 1993; Sundström et al. 2004; Frost et al. 2007), handling tests (e.g. Carere and van Oers 2004; Taylor et al. 2012) and open-field tests (e.g. Brown, Burgess, and Braithwaite 2007; Boon, Reale, and Boutin 2008) are commonly-used tests of boldness. Whereas these studies have the advantage of enhanced control, direct observational data documenting boldness under strictly natural conditions offers a means to assess simultaneously how this personality trait varies among free-

living individuals, and how it affects their fitness. But because boldness is difficult to quantify in naturalistic settings, few studies have used observational data to examine boldness (e.g. Reale et al. 2000), and only a small number of longitudinal studies of boldness have ever been conducted with free-living animals (e.g. Boon, Reale, and Boutin 2008; Reale et al. 2009). Here we conduct a longitudinal analysis of boldness among free-living spotted hyenas (*Crocuta crocuta*) in Kenya. The riskiest situations for spotted hyenas occur during encounters with lions. Hyenas and lions have a high degree of dietary overlap and compete for the same resources (Kruuk 1972; Hayward 2006). Due to their greater size and power, lions regularly steal kills from hyenas (Kruuk 1972; Mills 1990; Frank et al. 1995). Generally, interspecific competition between carnivores is particularly intense because of the specialized adaptations for killing possessed by these competitors (Creel et al. 2001). Lions represent a major source of hyena mortality; in studies of four separate populations of hyenas, lions were the largest sources of known hyena deaths in each population (Kruuk 1972; Trinkel et al. 2006; Watts & Holekamp 2009). In the Masai Mara, lion density is particularly high (Ogutu & Dublin 2002), suggesting that hyenas there may experience unusually frequent and intense competition with lions.

Despite the risks that lions pose to hyenas, hyenas do not necessarily avoid encounters with lions, and in fact they are often attracted to lions with kills, presumably due to the potential benefits of scavenging (Watts et al. 2010). Depending on the situation, such as the relative numbers of lions and hyenas present and whether or not a male lion is present, hyenas are sometimes able to steal parts of a carcass or even drive lions off a kill altogether (Kruuk 1972; Mills 1990). For hyenas, the possible benefits of acquiring food may outweigh the risk of injury or death from lions. Because proximity to lions represents both a risk and a potential

benefit to hyenas, measuring the behavior of hyenas during lion-hyena encounters offers a promising way to study boldness.

Previous research has suggested that individual spotted hyenas may vary in boldness and other related traits. In a study by Gosling (1998), observers were asked to rate captive hyenas on several personality traits; the study found that boldness was rated with very high reliability, but also found no evidence for a shy-bold continuum in the population using a principal components analysis. However, subsequent studies of free-living hyenas have suggested that consistent inter-individual differences in boldness do exist in spotted hyenas. A study by Watts et al. (2010) showed that there were significant individual differences in the way that hyenas responded to playbacks of lion roars. In this study, hyenas varied both regarding whether or not they avoided the roars, and also in the strength of their behavioral response to the playbacks. Watts et al. (2010) also demonstrated a correlation between boldness and vigilance behavior; hyenas that took more risks in response to the playback also tended to be more vigilant. These differences were context-specific, seen only in the context of interactions with lions, not at dens or in the “baseline” context in the absence of lions. Pangle (2008) reported evidence of consistent differences in vigilance behavior among adult hyenas, but not among juveniles.

Here, we examine the social, situational, and individual factors that contribute to boldness in spotted hyenas. Next we determine whether there is evidence for consistent individual differences in this trait, and determine how much of the phenotypic variation in boldness is due to heredity, non-genetic maternal effects, and permanent environmental

effects. We then examine the stability of boldness across ontogeny and across different contexts, and finally we evaluate the relationship between boldness and fitness.

METHODS

Study Subjects

Between 1988 and 2009, personnel from the Mara Hyena Project collected behavioral data on a group of free-living spotted hyenas, called the Talek Clan, in the Masai Mara National Reserve in Kenya (Boydston et al. 2001). All hyenas in this clan were recognized individually by observers based on their unique spot patterns, and were of known sex, age, and social rank. Hyenas were sexed based on the morphology of the glans of the erect phallus (Frank et al. 1990). We assigned ages to all natal animals (to ± 7 days) based on their appearance when they are first seen above ground at dens, and we were able to assign immigrant males' ages reliably (to ± 6 months) with an age-estimation model (Van Horn et al. 2003).

The social rank of each hyena in the clan was assigned using a dominance matrix based on observations of dyadic agonistic interactions (Holekamp & Smale 1993; Smale et al. 1993). Rank was reassessed each time a new animal reached adulthood, entered or left the clan, or died. Cubs were assigned the rank of their mother until they reached reproductive maturity at 24 months of age (Frank 1986; Glickman et al. 1992; Holekamp et al. 1997). We also calculated standardized rank for each hyena by dividing their numerical rank by the total number of ranked animals in the clan at the time.

We established maternity based on genotyping and observations of cubs nursing (Holekamp & Smale 1993). Paternity was assigned based exclusively on genotyping, as

previously described (Van Horn et al. 2004; Watts et al. 2011). Methods used to immobilize animals and collect blood samples for DNA extraction are described in detail in Engh et al. (2002). All sampling procedures were approved by the Institutional Animal Care and Use Committee at Michigan State University (AUF 07/08-099-00), complied with Kenyan law, and conformed to guidelines approved by the American Society of Mammalogists (Sikes & Gannon 2011).

Data collection

We generally observed hyenas daily from vehicles between 0530 and 0930 hours and between 1700 and 2000 hours. We initiated observation sessions whenever we saw a hyena or group of hyenas separated from others by at least 200 meters. Upon initiating an observation session, we recorded the GPS location of the session and conducted a behavioral scan that identified each hyena, noted its current behavior, and described its position in space; these scans were repeated every 20 minutes. During each session, we used critical incident sampling (Altmann 1974) to record specific behaviors such as aggressive acts, appeasements, vocalizations, and greetings. We also recorded whenever a hyena entered or left a session in progress. The presence, species, number, and sex of other carnivores present were also noted when possible, as was the presence of food in the possession of hyenas or other carnivores.

Observational data for this chapter were extracted from all sessions in which at least one known hyena and at least one lion were present simultaneously. During these sessions, we noted distances between each hyena and the lion or lions, both in regular scans at 20-minute intervals and during critical incident sampling. We also included distance data when it could be

reliably extrapolated from other data; for instance, if a hyena was recorded as “biting” a lion, a distance of zero meters was inferred. Distance data involving unidentified hyenas were not included in these analyses.

To assess boldness in hyenas, we measured two aspects of the behavior of each individual present during lion-hyena interactions. The first was the closest distance to which each hyena approached a lion (called the “minimum distance”) during a session. We also calculated the minimum standardized distance rank of each hyena; this was determined by ranking the minimum distances of all hyenas in a session from the closest to the farthest from lions, and dividing the distance rank of each hyena by the total number of hyenas with recorded distances in that session. This standardized measure allowed us to compare the behavior of individuals across very different circumstances. Hyenas that had smaller minimum distances and smaller minimum standardized distance ranks were considered bolder, because they were more prone to interactions with and attacks from lions than were other hyenas.

Other situational data were also collected from these sessions, including the maximum number of hyenas and lions present in the session, the time of day (either from midnight to noon, or from noon until midnight), whether or not food was available in the session, whether or not at least one male lion was present, and the current seasonal prey availability (high for June through October, and low from November through May).

Statistical Analysis

Situational factors influencing boldness

We assessed boldness based on two different levels of analysis; one at the level of the observation session, and another at the level of individual hyenas. First, we performed an analysis using the individual observation session as the unit of analysis to determine which social and environmental factors influence hyenas' distance from lions. In order to generate an accurate and unbiased dataset, we included only sessions in which at least three hyenas had known distances from the lion or lions. As the response variable for this session, we used an average of the minimum distances for all hyenas present in each session. This measure, calculated for each session, represented the average minimum distance that hyenas kept from lions during that session. Using this composite measure of boldness allowed us to assess the importance of situational variables that were common to all hyenas present in the session.

Using a Bayesian approach, we fitted a model with the Markov Chain Monte Carlo for Generalized Linear Mixed Models (MCMCglmm) analysis tool in the R statistical package (Hadfield 2010; R Core Development Team 2011), with the average minimum distance for all hyenas present in each session as the response variable, and various social and environmental aspects of the session as fixed effects. These fixed effects included the time of day, the ratio of the maximum number of hyenas present to the maximum number of lions present in the session, whether or not food was available in the session, whether or not at least one male lion was present, and whether seasonal prey availability was high or low. We included year and month as random effects. The posterior distribution of the model was sampled every 500 iterations after a burn-in period of 20,000 iterations for a total of 2,000 samples.

For all MCMCglmm models, the estimates are reported as modes of the posterior distribution, and we tested fixed effects for significance by determining whether or not the 95%

credible interval for the fixed effect included zero; variables for which the credible interval included zero were not significant predictors of boldness, whereas those that did not include zero were considered significant. We tested random effects for significance by comparing the deviance information criterion (DIC) values of models fitted with and without each random effect of interest; if the inclusion of a random effect lowered the DIC value of the model, the random effect was considered significant in predicting boldness.

For these models, we used a relatively uninformative prior that partitioned variance equally among all random effects (Hadfield 2010); using a more informative prior did not affect reported results. In these and the other MCMCglmm models described below, we assessed convergence by examining time series of the model parameters. We also inspected autocorrelation values for the models, all of which were less than 0.1 for reported values.

Consistency in boldness within individuals

We then performed a similar Bayesian analysis using individual hyenas as the units of analysis to (1) determine which characteristics of individuals affected the distances maintained by hyenas between themselves and lions, and (2) determine whether there was consistency across sessions within individuals in this measure of boldness.

In the individual-level analysis, we used hyenas' minimum standardized distance ranks from lions, rather than their absolute minimum distances from lions, as the measure of boldness. Here we only included sessions in which at least two hyenas had recorded distances, and we only included hyenas that had recorded distances from lions in at least four different observation sessions. We analyzed the boldness of males and females in separate models.

For each sex, we created a repeated measures MCMCglmm model with minimum standardized distance rank as the response variable. The standardized social rank and age of the hyena on the date of the session were included as fixed effects, and were tested for significance as described above. A unique session identifier was included as a random effect in both analyses to control for pseudoreplication. To determine whether individual hyenas were consistent in the minimum distances they maintained from lions, we tested whether the inclusion of a random effect representing the identity of the hyena improved the model by comparing DIC values. If this term significantly improved the fit of the model, individuals' behavior was considered consistent across sessions.

The posterior distribution of the model was sampled every 500 iterations after a burn-in period of 20,000 iterations for a total of 2,000 samples. For these models, we used an uninformative prior that partitioned variance equally among all random effects (Hadfield 2010); the results did not change when we used a more informative prior.

Heritability of boldness

To determine whether or not boldness is heritable in spotted hyenas, we created a restricted-likelihood Bayesian animal model (Kruuk 2004). Animal models use pedigree information to partition the heritable and non-heritable components of phenotypic variance (Kruuk 2004; Wilson et al. 2009). Phenotypic, additive genetic, maternal, and permanent environmental variances were estimated with a univariate-trait animal model predicting the boldness of each hyena. Permanent environment effects are created by each individual's environment and are consistent over its lifetime; maternal effects are non-genetic effects that a

mother has on all her offspring. We used the previously described model with individual hyenas as the units of analysis, but included boldness data from both sexes. We included all significant individual-level fixed effects as well as random effects representing the identity of the hyena, the session identifier, the identity of the hyena's mother, and a term representing the additive genetic effect. Because female hyenas mate with several males across their reproductive history, maternal effects can be distinguished from heritability via the effect of these different sires.

Because MCMCglmm requires values for all random effects, we generated unique maternal identities for immigrant males and natal animals with unknown mothers, following Taylor et al. (2012). This technique allows for the estimation of maternal effects, even when pedigree information is missing; however, it assumes that all hyenas with unknown maternity are unrelated.

We calculated heritability, maternal effects, and permanent environment effects by dividing the relevant variance component by the total phenotypic variance. Following Lessells and Boag (1987), we calculated repeatability by dividing the among-individual variance by the total among- and within-individual variance.

The posterior distribution of the animal model was sampled every 500 iterations after a burn-in period of 20,000 iterations for a total of 5,000 samples. For this model, we used an uninformative prior that partitioned variance equally among all random effects (Hadfield 2010); the results did not change when we used a more informative prior.

Stability over time and across situations

In order to determine whether the boldness of individual hyenas remained stable over time, we created generalized linear mixed models using the lme4 function in R. In each session, we determined whether each hyena with a recorded minimum distance was less or more than 24 months of age; hyenas that were less than 24 months of age were considered to be juveniles, and those over 24 months of age were considered to be adults. Only hyenas with at least two recorded distances in each age class were included in this analysis.

In these models, we used minimum standardized distance rank as the response variable and age class as the main fixed effect of interest. Other fixed effects described previously, including the hyena's sex and standardized rank, were also included in the analysis but only fixed effects that lowered the Akaike information criterion (AIC) value of the model were retained. Here again, a unique session identifier was included as a random effect in all models to control for pseudoreplication.

We included individual identity as a random intercept to allow for the variation in boldness between hyenas suggested by earlier analyses. We also added a random slope to the model, which described the extent to which the boldness of individual hyenas varied over time. If this term significantly improved the fit of the model, we concluded that boldness in hyenas was not a trait that changed consistently in individuals across ontogeny. To test whether the random slope significantly improved the fit of the model, we created two models that were identical except for the inclusion of the random slope. We then compared these two models with a log-likelihood ratio test, in which the log-likelihood ratio is calculated as $2[\log\text{-likelihood of model B} - \log\text{-likelihood of model A}]$, and tested as a chi-squared distribution (Pinheiro &

Bates 2000; Martin & Réale 2008). The approach of using random regression to investigate behavioral reaction norms is described in more detail in Dingemanse et al. (2010).

Using the same methodology, we ran a set of similar models to test whether the boldness exhibited by individual hyenas varied with prey availability. In these models, we used prey availability as the main fixed effect of interest, and defined the random slope to allow hyenas' boldness to change across sessions with high and low prey availability. Only hyenas present in at least two sessions in each prey availability category were included in this analysis.

Relationship between boldness and fitness

Finally we tested whether a female's boldness was related to fitness, as indicated by various measures of reproductive success and longevity. For these analyses, we used two lifetime measures of boldness: (1) a measure of relative boldness calculated by averaging all a hyena's minimum standardized distance ranks from lions during lion-hyena interactions, and (2) a measure of absolute boldness calculated by averaging all a hyena's actual minimum distances from lions during lion-hyena interactions.

As indicators of reproductive success, we used the total number of cubs borne by each female over her lifetime, as well as the number and proportion of her cubs that survived to three life-history milestones: den independence, weaning, and reproductive maturity. We created a set of generalized linear and second-order polynomial models with these fitness components as the response variables, and the lifetime boldness measure, maternal rank, and an interaction term as predictors. Only female hyenas that were born after our study began,

died before our study ended, and had recorded distances in at least two sessions with lions were included in this analysis.

We also used hyenas' longevity as a response variable to determine whether boldness is related to survival. For this dataset, we used the same two lifetime measures of boldness, but included only females for which we had known death dates and had recorded distances in at least two sessions with lions. We created both generalized linear and second order polynomials with longevity (in months) as the response variable. As fixed effects, we included our lifetime boldness measures and average lifetime standardized rank, as well as the interaction terms between these variables.

For longevity and all measures of reproductive success, we used likelihood ratio tests to determine whether the second-order polynomial models were able to predict these fitness measures better than linear models. All variables in these analyses were Z-transformed.

RESULTS

Situational factors influencing boldness

Between 1988 and 2009, there were 128 sessions with recorded minimum distances that met our criteria for inclusion in this analysis. In these sessions, the average hyena-to-lion ratio was 6.13 ± 0.634 , and male lions were present in 34.4% of these sessions. The average minimum distance between hyenas and the lion or lions present was 24.51 ± 3.24 meters. On average, there were 8.50 ± 0.61 hyenas with recorded minimum distances from lions in each of these sessions. In general, hyenas approached lions more closely as the hyena-to-lion ratio increased and when food was present in a session (Table 2.1). Hyenas maintained greater

distances from lions when at least one male lion was present (Table 2.1). Time of day and seasonal food availability were not significant predictors of the average minimum distance in these sessions, although there was a non-significant trend for larger minimum distances from noon to midnight than from midnight to noon (Table 2.1).

Table 2.1

Fixed effects predicting average minimum distances from hyenas to lions in sessions with at least one lion present and at least three minimum distances for known hyenas.

Coefficients	Posterior mode	95% credible interval	p _{MCMC}
(Intercept)	67.9058	(33.5133 to 98.7528)	<0.001*
Time of day (PM)	14.8892	(-2.6071 to 30.7114)	0.08
Hyena-to-lion ratio	-1.4121	(-2.5021 to -0.3243)	0.016*
Male lion present	16.5883	(2.1574 to 32.4285)	0.034*
Food available	-28.9227	(-55.9679 to -3.9985)	0.034*
Prey availability (low)	-3.1148	(-17.8168 to 11.5887)	0.664

Including a random effect of year improved the fit of the model (DIC=938.24) compared to models that included random effects of both year and month (DIC=939.54), only month (DIC=941.69), or neither random effect (DIC=939.21), indicating that the year affects the general boldness of hyenas in some way.

Consistency in boldness within individuals

In our repeated measures analysis, there were 43 females that ranged in age from 9.87 to 198.80 months, averaging 66.32 ± 2.00 months, and 32 males that ranged in age from 10.13 to 165.90 months, averaging 77.37 ± 2.32 months.

For males, none of the individual-level predictor variables were significant; neither age nor standardized rank affected how closely male hyenas approached lions (Table 2.2). For

females, age was not a significant predictor of boldness, but higher-ranking hyenas tended to approach lions more closely than did lower-ranking hyenas (Table 2.3).

Table 2.2

Fixed effects predicting the minimum distance separating each male hyena from lions.

	posterior mean	95% credible interval	p _{MCMC}
(Intercept)	0.4242757	(0.3198692 to 0.5258341)	<0.001*
Standardized rank	0.11127	(-0.0467974 to 0.2601023)	0.160
Age	-0.0004126	(-0.0013439 to 0.0004587)	0.376

Table 2.3

Fixed effects predicting the minimum distance separating each female hyena from lions.

	posterior mean	95% credible interval	p _{MCMC}
(Intercept)	0.3798397	(0.2953735 to 0.4660331)	<0.001*
Standardized rank	0.2244043	(0.0235000 to 0.4879079)	0.044*
Age	0.000239	(-0.0006693 to 0.0010733)	0.594

For females, including a random effect of an individual identifier improved the fit of the model (DIC=147.87), compared to a model that included only the session identifier as a random effect (DIC=160.84), indicating that individual females have consistent boldness measures across sessions. For males, the inclusion of a random effect of an individual identifier did not improve the model (DIC=120.44), compared to a model without this term (DIC=119.78), suggesting that males are not consistent across sessions in their boldness.

Heritability of boldness

Genetic effects, maternal effects, and permanent environment effects were all significant for boldness, as indicated by a lower DIC value when these effects were included

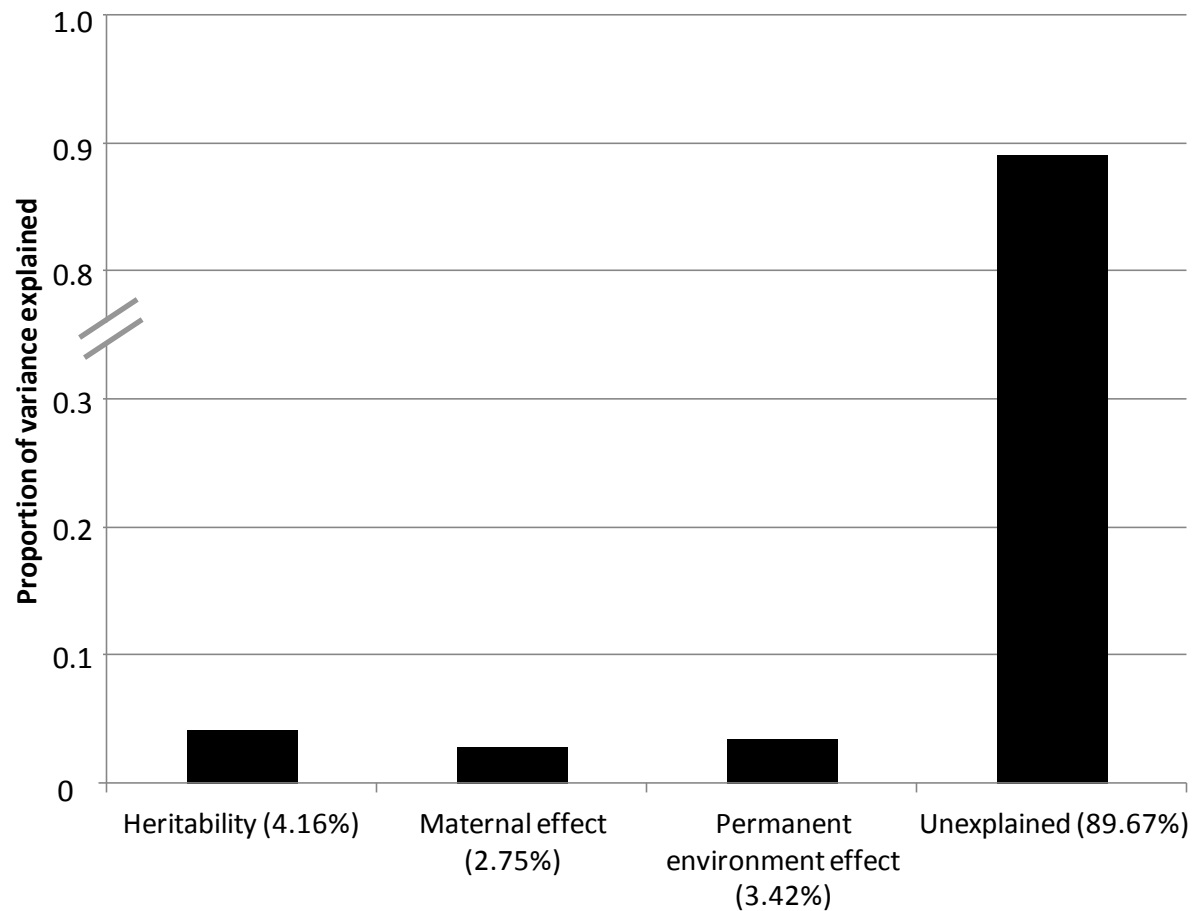


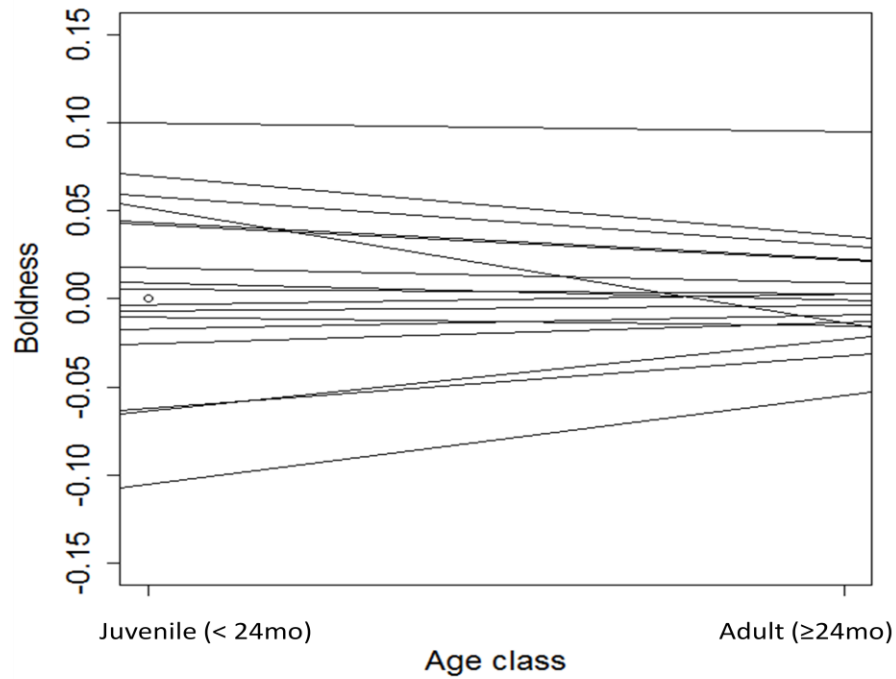
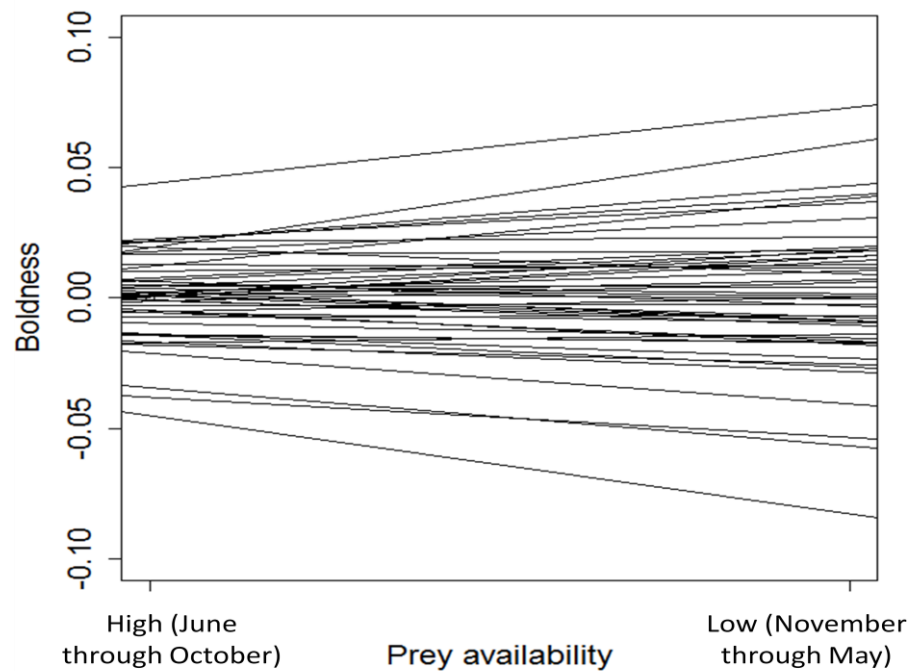
Figure 2.1. The percent of variation in boldness attributable to heritability, permanent environment effects, maternal effects, and the remaining unexplained variation. Variances were estimated with a MCMCglmm animal model. Values on the y-axis between 0.3 and 0.8 are omitted.

in a model (DIC= 296.912), compared to when they were omitted (genetic effect omitted, DIC=304.211; maternal effect omitted, DIC=-302.640, permanent environment effect omitted, DIC=302.332). The heritability estimate was 0.0416 (95% CI=0.0116 to 0.0770, Figure 2.1), the permanent environment estimate was 0.0342 (95% CI=0.0141 to 0.0744, Figure 2.1), and the maternal effect estimate was 0.0275 (95%CI=0.0115 to 0.0665, Figure 2.1). The estimate for repeatability was 0.0682 (95% CI=0.0417 to 0.1271).

Stability over time and across situations

There were 17 hyenas present with lions in at least two sessions during each age interval; 12 (70.6%) were female and 5 (29.4%) were male. The model including a random slope of age class in addition to the random intercept was not significantly better at predicting the boldness of individuals than the model with only the random intercept (LRT=0.301, df=2, p=0.860). The inclusion of a random slope was not significant, indicating that the boldness measures of individual hyenas generally change in a consistent way with age (Figure 2.2a).

There were 49 hyenas that met our criteria for the prey availability analysis. Of these hyenas, 27 (55.1%) were female and 22 (44.9%) were male. For this analysis, including a random slope of prey availability did not improve the fit of the model (LRT=-0.757, df=2, p=1). The inclusion of a random slope was not significant, indicating that the boldness measures of individual hyenas generally change in a consistent way across varying levels of prey availability (Figure 2.2b).

a**b**

Figures 2.2a and 2.2b. Predicted behavioral reaction norms for boldness measures across (a) two age classes and (b) two categories of seasonal prey availability, as predicted by lmer models. Each line represents how the behavior of an individual changes across categories. Smaller relative boldness measures represent bolder individuals, since these measures are based on minimum distances to lions.

Relationship between boldness and fitness

Thirty females satisfied the criteria for inclusion in our analysis of reproductive success. Using generalized linear models, neither the lifetime measure of relative boldness nor the lifetime measure of absolute boldness was significant in predicting any measure of reproductive success ($p > 0.2$). No interaction terms containing either boldness measure improved the fit of the reproductive success models, and second-order regression models were not better at predicting reproductive success than linear models ($p > 0.2$).

There were 40 female hyenas that satisfied the criteria for our analysis of longevity. The age at death of hyenas ranged from 41.23 to 212.73 months, with an average of 106.82 ± 6.75 months. Using generalized linear models, neither the lifetime measure of relative boldness nor the lifetime measure of absolute boldness was significant in predicting longevity ($p > 0.2$). Standardized rank was not a significant predictor of age at death ($p = 0.684$). No interaction terms containing either boldness measure improved the fit of the generalized linear longevity models. Interestingly, however, a second-order polynomial model with lifetime relative boldness was significantly better at predicting age at death than a corresponding linear model ($LRT = 4.488$, $df = 1$, $p = 0.034$, Figure 2.3). In this model, the second-order boldness term was significant in predicting females' age at death (-467.402 ± 222.995 , $t = -2.096$, $p = 0.043$).

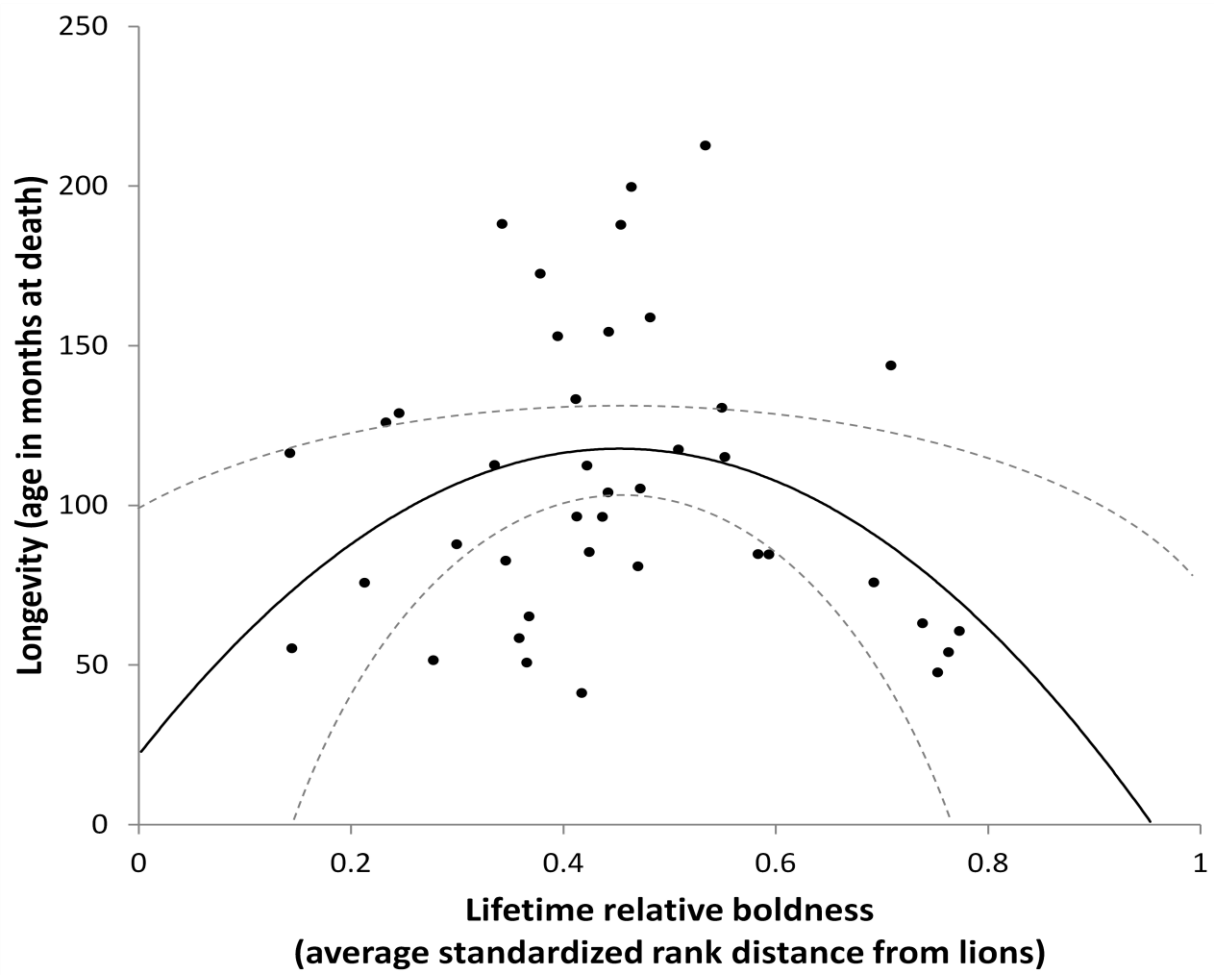


Figure 2.3. The relationship between lifetime relative boldness and longevity. Actual values are displayed as dots, and the values predicted by the second-order regression model are shown as a line, with 95% confidence intervals indicated with grey dotted lines.

DISCUSSION

Overall, we found that there are consistent inter-individual differences in lion-related boldness in female spotted hyenas, but not in males. This finding is consistent with previous research on other species (guppies, Harris et al. (2010); field crickets, Hedrick and Kortet (2012)), where males also failed to show consistency in boldness across repeated observations. Female and male hyenas may employ different strategies in terms of boldness, with females being more consistent and males maintaining more situational plasticity. Because immigrant male hyenas hold lower social ranks, and therefore have reduced access to resources, a less rigid and more adaptable strategy might be advantageous for males. Males have less reliable access to food, smaller body sizes, and higher movement and activity rates than females, all of which may make them more sensitive to environmental conditions than females (Kruuk 1972; Mills 1990; Kolowski et al. 2007).

Several situational aspects of lion-hyena interactions, such as the time of day and the availability of food were important determinants of boldness among hyenas. We found that the presence of at least one male lion and the hyena-to-lion ratio both affected the behavior of hyenas, consistent with previous findings on lion-hyena interactions (Kruuk 1972; Cooper 1991). Not surprisingly, hyenas were bolder when food was available in a session, supporting the hypothesis that access to food is a major incentive for hyenas to interact with lions, despite the risks involved (Watts et al. 2010).

Social rank had no effect on boldness among males, but we found that higher-ranking females tended to approach lions more closely than did lower-ranking females. This is somewhat surprising in terms of the relationship between boldness and resource availability, as

females with restricted access to food might be expected to take more risks than those with better access to food (Riesch et al. 2009). However, high-ranking females would gain possession of any scraps or carcasses stolen from lions, so they may actually benefit the most from approaching and interacting with lions. Even if food is successfully scavenged from lions, low-ranking hyenas might be prohibited from feeding by higher-ranking individuals.

Our population-wide repeatability estimate was significant but small, compared to estimates for other personality traits (Bell et al. 2009). Although this estimate may be accurate, the low value may also be partially due to statistical artifacts. Generally, when estimating repeatability from repeated measures, the experimenter assumes that the conditions remain constant over each trial. In laboratory experiments this is often a reasonable assumption, but in the field there are innumerable conditions that change between trials for which we could not account in our study. Additionally, the low repeatability measure may be due to the inclusion of males in the animal model. Data from immigrant males are necessary to estimate heritability, but we found no evidence of consistent differences in boldness among males in an earlier analysis, and it is possible that the inclusion of these values decreased the repeatability estimate here.

The heritability estimate from our animal model was also low but significant. This estimate is much lower than the average heritability for behavioral traits (0.30 ± 0.02) (Mousseau & Roff 1987), but is within the range of reported values in the literature. Sinn, Apiolaza, and Moltschaniwskyj (2006) reported a boldness heritability estimate of 0.05, and estimates from Bell (2005) were as low as 0.002. However, repeatability generally sets an upper limit for heritability (Falconer 1981), and in light of our small repeatability estimate, our

heritability estimate is relatively substantial. Statistically, traits with low repeatabilities tend to give underestimates of heritability and other important quantitative genetic parameters (Whitlock 1998). Estimates for both maternal effects and permanent environment effects for boldness in our study were both small, but significant. As noted previously, differences between heritability and maternal effect estimates were due to sire effects within dams.

While we were able to explain a small amount of the observed phenotypic variation in boldness via heritability, maternal effects, and permanent environment effects, more than 89% of the observed variation in boldness was unexplained by the model. None of the three sources of inter-individual variation that we assessed appear to play a large role in boldness in hyenas. Lion-hyena interactions are complex and dynamic, and there are many environmental and social conditions that we could not include in our models or even measure accurately in the field, such as motivational states and events preceding the lion-hyena interaction. It is likely that these factors are responsible for much of the observed variation for which we could not account statistically in our analyses.

Random regressions showed that the distances hyenas maintain from lions are relatively stable over time and varying circumstances. Boldness was consistent across age classes, as indicated by the fact that the rank order of the boldness of individual hyenas remained relatively stable over time. In other words, hyenas that were bold as juveniles were also generally bold as adults, suggesting that the boldness of an individual is determined relatively early in life. Research on other species has also found evidence of ontogenetic consistency in boldness (great tits, Carere et al. 2005; fishing spiders, Johnson & Sih 2005; dumpling squid, Sinn et al. 2008).

A similar trend was found across varying levels of seasonal prey availability; hyenas that were relatively bold when prey was abundant were also bolder than their peers when prey was scarce. This finding, along with the earlier finding that prey availability does not affect general boldness levels in hyenas, was somewhat surprising, since boldness behavior is predicted to change with hunger levels (Riesch et al. 2009). When food is hard to come by, the potential benefits of approaching and interacting with lions are expected to increase; however, our results showed no difference in boldness between seasons of high and low prey availability, and no difference between individuals in how they respond to these changes. It is possible that our measure of seasonal prey availability did not accurately reflect the amount of food available to hyenas on a fine enough time scale here. Boldness may be also constrained in some way, and the hyenas' behavior may not be sufficiently labile to adjust to differing levels of prey abundance. The genetic, cognitive, or physical constraints underlying personality traits such as boldness may prohibit individuals from behaving optimally in any given situation (Sih et al. 2004b; Sih et al. 2004c; Dingemanse & Reale 2005; Dochtermann & Roff 2010). Due to one or more of these constraints, behavior in one environment might be optimal, whereas the behavior may seem suboptimal, or even maladaptive, in a different context. While none of these factors were tested in our analyses, future research that investigated constraints on boldness among hyenas might be beneficial.

We found that, although boldness was not correlated with the reproductive success of female hyenas, it was significantly related to longevity. We found evidence of stabilizing selection on boldness; females that were particularly bold and those that were particularly shy had shorter lifespans than did those in the middle of the shy-bold continuum. Hyenas that

consistently approach lions closely may be more prone to injury and death than those that maintain greater distances from lions. Meanwhile, hyenas that stay relatively far from lions may suffer because they do not reap the same benefits that bolder hyenas are able to procure.

Because we only measured boldness in hyenas in one context in this study, it is not possible to draw conclusions about this trait in contexts other than lion-hyena interactions. It would be beneficial for future researchers to examine other types of boldness in hyenas, such as boldness related to mating, dispersal, or anthropogenic influences. Future studies should also test boldness in hyenas with experiments in the field; it would then be possible to compare experimental measures of boldness with the reliable observational estimates measured here, to determine whether there is consistency between these two measures.

This study confirms the existence of individual differences in boldness among female spotted hyenas that are consistent over ontogeny and across contexts. We found that a small but significant proportion of the variation in boldness behavior was due to heritability; this effect may be smaller than effects in other species because the spotted hyena is a predator, and thus faces a very different set of tradeoffs than do prey species. Whereas prey species rarely have anything to gain from approaching and interacting with their predators, hyenas can potentially benefit greatly from interactions with lions by acquiring food, despite the risk of injury or death. Differences among hyenas in boldness may reflect plastic individual strategies aimed at resource acquisition, rather than direct genetic effects. However, stabilizing selection may limit extreme boldness or shyness in this species, because hyenas with intermediate phenotypes survive longer than those on either extreme end of the boldness spectrum.

Understanding boldness in hyenas and other large carnivores can potentially inform our understanding and treatment of "problem individuals" (Linnell et al. 1999). Carnivores are especially prone to causing problems for herders, ranchers, and other humans living in or near undeveloped land; hyenas, wolves, lions, and other predators are known to prey on livestock and pets (Patterson et al. 2004; Kolowski & Holekamp 2006; Darrow & Shivik 2009). It has been suggested that that boldness may play a role in the likelihood of depredation (Linnell et al. 1999; Darrow & Shivik 2009). This study represents only the first step in understanding patterns of boldness among hyenas, but future studies of boldness in large carnivores might be able to determine which individuals in each species are more likely to cause problems associated with livestock or pet depredation, and may thus be able to suggest new ways to mitigate and manage these problems in ways consistent with conservation goals.

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CHAPTER 3

INDIVIDUAL DIFFERENCES IN AGGRESSIVENESS AMONG SPOTTED HYENAS

INTRODUCTION

Aggression is one of the most noticeable and fundamental aspects of behavior; extensive research has been conducted on when, why, and how animals behave aggressively toward one another (e.g. Smith and Price 1973; van den Berghe 1974; Francis 1988; Hemelrijk 2000; Panksepp and Zellner 2004). However, until recently, much of the focus of aggression research was at the level of species (e.g. Grant & Ulmer 1974; Yasukawa & Searcy 1982; Thierry 1985; Digby 1999), while far fewer studies examined behavioral differences among individuals within a population. In the last several years, research on animal personality has begun to address consistent inter-individual differences in aggressive behavior, revealing that these differences may be stable across time and contexts and can have a significant impact on fitness (Dingemanse & de Goede 2004; Johnson & Sih 2005; Bell & Sih 2007; Boon et al. 2008; Sinn et al. 2008).

Male animals are generally considered to be more aggressive than females, because in many species, competition for mates selects for large, aggressive males (Geist 1974; Walters & Seyfarth 1987; Archer 1988; Kunc et al. 2006). Thus, many studies of inter-individual differences in aggressiveness have focused on species in which either males are the more aggressive sex, or males and females emit aggressive behaviors at similar rates (e.g. Leshner and Moyer 1975; Armitage 1986; Verbeek, Boon, and Drent 1996; Taylor et al. 2012). However, females also often fight with one another over resources and in defense of their young, and the

aggressiveness of females may be generally underestimated (Sandell 1998; Bebié & McElligott 2006; Clutton-Brock 2007; Van Meter 2009). Extreme cases of aggressive behavior in females present themselves in species with sex role reversals, in which females are socially dominant to males (e.g. Kappeler 1990; Gwynne 1991; Delehanty et al. 1998; Berglund and Rosenqvist 2003). In these species, individual differences in aggressive behavior may have very different patterns, and the fitness consequences of this variation may be very different from those documented in species in which males dominate females. To date, we know of no studies investigating the personality trait of aggression in a female-dominated mammal. Here we examine inter-individual differences in aggression in a highly aggressive and female-dominated carnivore, the spotted hyena (*Crocuta crocuta*). Hyenas offer an excellent model system in which to study aggressive behavior because aggression in this species is very frequent, is easily observable, varies in intensity, and occurs in several different contexts. Additionally, because the hyenas in our study population have been monitored continuously since 1988, we have genetic and fitness data with which we can assess the causes and consequences of aggressiveness in this species.

Research on sex differences in the consistency of aggression has been inconclusive in both humans and other animals. Whereas some studies (e.g. While et al. 2010) have found that behavioral consistency does not differ between the sexes, a meta-analysis by Bell et al. (2009) found that differences between males and females in behavioral repeatability vary based on the species and the traits being studied. This suggests that, in terms of consistency, the optimal strategy for each sex may be determined separately for each species based on specific aspects of its environment, life history, and morphology.

Although there is a general consensus that inter-individual differences in aggressiveness exist in many species (e.g. marmots: Armitage 1986; sticklebacks: Bakker 1986; great tits: Verbeek, Boon, and Drent 1996; red squirrels: Boon, Reale, and Boutin 2008), there is much debate as to whether aggressiveness is domain-general or context-dependent. In other words, are individuals that are aggressive in one context also aggressive in another (i.e. domain-general), or is aggressiveness in different contexts unrelated (i.e. context-specificity)? In female fishing spiders, aggression is stable across contexts; individuals that are highly aggressive in a food-related context are also more likely to engage in precopulatory cannibalism (Johnson 2001; Johnson & Sih 2005). However, research suggests that aggression in some insect species is context-specific based on the identity of the opponent (Pfennig & Reeve 1989; Tanner & Adler 2009). Contexts of aggression have also received a significant amount of attention in humans; most psychologists agree that aggression in humans is context-specific (for reviews, see Buss and Shackelford 1997 and Kagan 2003). However, there are few studies addressing the effect of context on aggressive behavior in non-human mammals.

Artificial selection for short or long attack latency in house mice has been very successful, indicating that there is a strong genetic component to aggressiveness (Benus et al. 1991; Miczek et al. 2001). A study of aggressiveness in captive vervet monkeys estimated the heritability of aggressiveness in that species to be 0.64 (Fairbanks et al. 2004). However, other studies, especially those with free-living subjects, have generally yielded lower estimates of heritability. For instance, Taylor et al. (2012) estimated that only 12 percent of the phenotypic variation in aggressive behavior observed in wild red squirrels could be explained by genetics,

and Bell (2005) estimated that the heritability of aggressiveness in some populations of sticklebacks may be as low as 0.01.

Studies of the fitness consequences of aggressiveness have also produced conflicting results; whereas aggression enhances reproductive success in some species, it decreases some aspects of fitness in others. For instance, a study of aggressiveness in wild skinks showed that the offspring of particularly aggressive females had enhanced survival, compared to the offspring of less aggressive females (Sinn et al. 2008). By contrast, in western bluebirds, aggressiveness in males was linked to lower reproductive success; males that defended their nests most intensely fledged fewer offspring than other males, due to a tradeoff between aggression and parental care (Duckworth 2006). Finally, Packer et al. (1995) found that despite having shorter interbirth intervals and increased infant survival, aggressive female baboons of high social rank had reduced fertility and a higher incidence of miscarriages.

Among hyenas, adult females are larger than adult males by about 10 percent, and are socially dominant to immigrant males (Kruuk 1972). Within a clan, there is a rigid linear dominance hierarchy, and social status is reinforced through frequent aggressive behaviors (Kruuk 1972; Frank 1986; Mills 1990). Rank determines access to resources, and competition among clan members for food is intense; aggression over food occurs frequently, as high-ranking females frequently direct food-related aggression toward lower-ranking clan members (Kruuk 1972; Mills 1990; Frank et al. 1995). Aggressive behavior also commonly occurs in contexts unrelated to food; in fact much aggression appears to be entirely unprovoked, apparently functioning mainly to maintain the status quo in the social hierarchy (Van Meter 2009). Another common form of non-food-related aggression occurs during maternal

interventions, in which a mother directs aggression toward conspecifics in defense of her offspring (Holekamp & Smale 1991; Engh et al. 2000).

The aggressive behavior of female hyenas differs markedly from that of male hyenas. Female hyenas direct aggression toward conspecifics almost three times more often than do males, although the rate at which female hyenas emit aggressions is not higher than that of most female primates (Van Meter 2009). Additionally, although male hyenas exhibit intra-sexual aggression at a low level (Van Meter 2009), with the exception of “baiting” behavior, males very rarely direct aggressions toward females (see Szykman et al. 2003). Thus, although we know that female hyenas are more aggressive than males, we lack information on variation in aggressiveness within each sex; we do not know how aggressive behavior varies among either females or males.

Previous research has shown that hormones influence aggressive behavior in hyenas via maternal effects. Dloniak et al. (2006) found that cubs born to mothers with higher androgen concentrations during pregnancy exhibited more aggressive behavior than those born to pregnant females with lower androgen levels. Van Meter (2009) also found a positive correlation between maternal fecal androgen levels during pregnancy and rates at which offspring emitted aggressive acts as adults, suggesting an organizational role for hormones in shaping aggressiveness in hyenas. However, beyond this maternal effect, we know very little about the causes of inter-individual variation in aggression in this species.

Much of the variation in reproductive success among female spotted hyenas is driven by social rank. High-ranking females begin breeding at younger ages and have shorter interbirth intervals, longer reproductive life-spans, and more surviving offspring than do lower-ranking

females (Holekamp & Smale 1996; Swanson et al. 2011). However, low-ranking individuals benefit more than high-ranking individuals do from high prey availability in terms of reproductive success. Whereas high-ranking hyenas had enhanced reproductive success at all times, low-ranking hyenas enjoyed better reproductive success when prey abundance was high than when prey were scarce. Together, these results suggest that increased access to resources drives reproductive performance in hyenas, so it is possible that more aggressive hyenas experience better reproductive success than less aggressive ones due to a superior ability to monopolize resources.

In this chapter, we examine two types of aggressive acts: food-related aggressions and non-food-related aggressions. We first determine which situational and individual factors influence aggressive behavior among hyenas. Then, we inquire whether there is evidence of consistent differences among individuals in two measures of aggressiveness, and whether these differences are heritable and subject to maternal effects. We also assess the stability of aggressiveness over time and across contexts, and we conclude with an evaluation of the relationship between aggressiveness and fitness.

METHODS

Study Subjects

Between 1988 and 2009, personnel from the Mara Hyena Project collected behavioral data on a large group of free-living spotted hyenas, called the Talek Clan, in the Masai Mara National Reserve, Kenya (Boydston et al. 2001). All hyenas in this clan were recognized individually by observers based on their unique spot pattern and were of known sex, age, and

social rank. Hyenas were sexed based on the morphology of the glans of the erect phallus (Frank et al. 1990). We assigned ages to all natal animals (to ± 7 days) based on their appearance when they were first seen above ground at dens, and we were able to assign the ages of immigrant males reliably (to ± 6 months) with an age-estimation model (Van Horn et al. 2003).

The social rank of each hyena in the clan was assigned using a dominance matrix based on observations of dyadic agonistic interactions (Holekamp & Smale 1993; Smale et al. 1993). Rank was reassessed each time a new animal reached adulthood, entered or left the clan, or died. Each cub was assigned the rank of its mother until it reached reproductive maturity at 24 months of age (Frank 1986b; Glickman et al. 1992; Holekamp et al. 1997); at that time young females were assigned their own ranks in the adult hierarchy. We calculated standardized rank by dividing each hyena's numerical rank by the total number of ranked animals in the clan at the time.

We established maternity based on genotyping and observations of cubs nursing (Holekamp & Smale 1993). Paternity was assigned based exclusively on genotyping, as previously described (Van Horn et al. 2004; Watts et al. 2011). Methods used to immobilize animals and collect blood samples used for DNA extraction are described in detail in Engh et al. (2002). All sampling procedures were approved by the Institutional Animal Care and Use Committee at Michigan State University (AUF 07/08-099-00), complied with Kenyan law, and met guidelines approved by the American Society of Mammalogists (Sikes & Gannon 2011).

Data collection

We generally observed hyenas daily from vehicles between 0530 and 0930 hours and between 1700 and 2000 hours. We initiated an observation session whenever we saw one or more hyenas separated from others by at least 200 meters. Upon initiating an observation session, we recorded the GPS location of the session and conducted a behavioral scan that identified each hyena and noted its current behavior; these scans were repeated every 20 minutes. During each session, we used critical incident sampling (Altmann 1974) to record specific behaviors such as aggressive acts, appeasements, vocalizations, and greetings. We also recorded whenever a hyena entered or left a session in progress.

We used three different measures of aggressiveness: (1) the intensity of particular aggressive acts within observation sessions, (2) the aggression 'count' for each individual within each observation session, and (3) the lifetime hourly aggression rate calculated over all observations sessions in which an individual was seen during its adulthood. Aggression intensity was a measure of the severity of an aggressive act, measured on a scale of 1 to 3. Aggressive acts with intensities of 1 were low-intensity threats characterized by an intention movement to bite. Aggressive acts with intensities of 2 were intermediate-intensity threats involving snapping or lunging, but no actual contact. Aggressive acts with intensities of 3 were high-intensity threats involving a biting attack. An aggression count measured how many times a hyena emitted aggressive acts during a session. Following Van Meter (2009), we also calculated an hourly adjusted aggression rate for each individual present in each session as:

$$\frac{\text{number of aggressive acts} \div \text{number of potential targets}}{\text{number of hours the session lasted}}$$

where the number of potential targets was a count of all lower-ranking hyenas present. This measure controlled for variation in the number of opportunities each hyena had to emit aggressive acts during each session. To calculate a lifetime aggression rate for each hyena, we averaged its adjusted aggression rates in all its sessions after reaching reproductive maturity at 24 months of age.

Aggressions were categorized as either food-related or non-food-related, and aggression intensities, counts, and rates for these two contexts were treated separately. Food-related aggressions included all aggressive behaviors that took place in the presence of food. All other aggressions were considered non-food aggressions. In this study, we used the abbreviation NFA (for “non-food aggression”) to refer to aggressive acts occurring under circumstances not associated with food, and FA (for “food-related aggression”) to refer to aggressive acts occurring in the presence of food at dens, fresh kills, and at older carcasses.

Only dyadic aggressive interactions, and only aggressive acts directed down the hierarchy (i.e. at lower-ranking hyenas), were included in our analyses. When individuals had no lower-ranking targets present in a session, we did not include aggression counts or rates for them in that session, as they could not emit any aggressions down the hierarchy. Additionally, for adult females, we only included sessions in which an individual was lactating, because aggression levels vary with reproductive state among female hyenas (Van Meter 2009). Females were considered to be lactating between the date of birth of their last litter and the first of three milestones: (1) the date of conception of the next litter, (2) the date of weaning of the last litter, or (3) the disappearance of the last litter (Holekamp & Smale 1996).

Specific situational data were collected from all observation sessions, including the location of the session (a fresh kill, an old carcass, the communal den, a mating event, or “other” location), the time of day (either from midnight to noon, or from noon until midnight), the duration of the session, the maximum number of hyenas present, and the seasonal prey availability (high for June through October, and low from November through June).

We calculated the age (in months) and standardized rank of each hyena present in each session. Additionally, for each hyena in each session, we divided the number of lower-ranking hyenas present by the total number of hyenas present in the session; this measure is referred to as the proportion of hyenas present that were potential targets of aggression.

Statistical Analysis

Bayesian analyses

For many of our analyses, we adopted a Bayesian approach and created models with the Markov Chain Monte Carlo for Generalized Linear Mixed Models (MCMCglmm) analysis tool in the R statistical package (Hadfield 2010; R Core Development Team 2011). For each of these analyses, we tested fixed effects for significance by determining whether or not the 95% credible interval for the fixed effect included zero; variables for which the credible interval included zero were not significant predictors of the response variable, whereas those that did not include zero were considered significant. We tested random effects for significance by comparing the deviance information criterion (DIC) values of models fitted with and without the random effect of interest; if the inclusion of a random effect lowered the DIC value of the model, the random effect was considered significant in predicting the response variable.

For zero-inflated MCMCglmm models, we began by using a saturated model with fixed effects contributing to both the poisson and zero-inflated portions of the model, but only retained zero-inflation terms that lowered the DIC value of the model. In the zero-inflated portion of the model, the estimates for fixed effects were interpreted as the $\log(e)$ of the ratio of the odds of the response variable not occurring compared to the odds of the response variable occurring.

For all MCMCglmm models, we used a relatively uninformative prior that partitioned variance equally among all random effects (Hadfield 2010); using a more informative prior did not affect reported results. We assessed convergence of these models by examining time series of the model parameters. The estimates are reported as posterior means, with 95% credible intervals. We also inspected autocorrelation values for these models, all of which were less than 0.1 for reported values.

Situational factors influencing aggressiveness

We assessed aggressiveness based on two different levels of analysis; one at the level of the observation session, and another at the level of individual hyenas. First, we performed analyses using the observation session as the unit of analysis to determine which social and environmental factors influenced hyenas' aggressiveness.

Aggression count

For each session, we counted the total number of NFAs emitted. In sessions where food was present, we also counted the total number of FAs emitted during the session. These measures represent the general food-related and non-food-related aggressiveness of hyenas

present in each session. We used these two measures as response variables in two zero-inflated MCMCglmm models. We ran separate session-level models for FAs and NFAs, because particular situational factors may influence these two types of aggressions in different ways. We included various situational aspects of the session as fixed effects, including the location and duration of the session, the time of day, the maximum number of hyenas present, and the seasonal prey availability.

Data for these analyses included only aggressive acts emitted by adult hyenas. To reduce the number of zeros and encourage model convergence, in these analyses we did not include sessions that were less than ten minutes long. The posterior distribution of the model was sampled every 500 iterations after a burn-in period of 20,000 iterations for a total of 2,000 samples. We used a one-way Kruskal Wallis ANOVA test to determine whether the mean FA count and mean NFA count differed significantly.

Aggression intensity

We also ran separate session-level models using the average FA intensity and the average NFA intensity exhibited by all hyenas in the session as the response variables, with the same fixed effects described above. Only aggressive acts emitted by adults were included in this analysis, and sessions of all lengths during which aggression occurred were included. The posterior distribution of the model was sampled every 500 iterations after a burn-in period of 15,000 iterations for a total of 2,000 samples. We used a one-way Kruskal Wallis ANOVA test to determine whether the mean FA intensity and mean NFA intensity differed significantly.

Consistency in aggressiveness within individuals

We then performed similar Bayesian analyses using individual hyenas as the units of analysis to (1) determine which characteristics of individuals affected aggressiveness, and (2) determine whether there was consistency within individuals in aggressiveness across repeated observations.

Aggression count

In the first two repeated measures analyses, we used the FA and NFA counts for each hyena in each session as the response variables in zero-inflated poisson MCMCglmm models. We included the sex of the hyena, its standardized social rank, its age at the time of the session, and the proportion of targets in the session as fixed effects in these individual-level models. In these models, we only included adults appearing in at least 20 sessions with potential targets for either FAs or NFAs. Because of the large number of zeros, we only included aggression counts from sessions that were at least 30 minutes long, and we omitted data from sessions in which no aggressive interactions occurred.

A unique session identifier was included as a random effect to control for pseudoreplication. To determine whether individual hyenas were consistent in their aggressiveness, we also included a random effect representing the identity of the aggressor. If this random effect of individual identity significantly improved the fit of the model, individuals' behavior was considered consistent across sessions. The posterior distribution of the model was sampled every 500 iterations after a burn-in period of 20,000 iterations for a total of 2,000 samples.

Aggression intensity

We then created similar individual-level models for FAs and NFAs emitted by adults, using the intensity of each type of aggressive act as the response variables, with the same individual-level fixed effects as described above. We carried out separate analyses for males and females. The posterior distribution of the model was sampled every 100 iterations after a burn-in period of 10,000 iterations for a total of 1,000 samples.

Heritability of aggressiveness

To determine whether or not aggressiveness is heritable in hyenas, we created restricted-likelihood Bayesian animal models for several measures of aggressiveness (Kruuk 2004). Animal models use pedigree information to partition the heritable and non-heritable components of phenotypic variance (Kruuk 2004; Wilson et al. 2009). Phenotypic, additive genetic, maternal, and permanent environmental variances were estimated with univariate trait animal models predicting NFA and FA measures for each hyena. Permanent environment effects are created by each individual's environment and are consistent over its lifetime; maternal effects are non-genetic effects that a mother has on all her offspring. Because female hyenas mate with several males across their reproductive history, maternal effects can be distinguished from heritability via the effect of these different sires.

We carried out separate analyses for FA intensity, NFA intensity, lifetime FA rate, and lifetime NFA rate. In the intensity models, we used the same fixed effects as in the individual-level models described above. In the lifetime aggression rate models, we included only sex and lifetime standardized rank as fixed effects. We retained only fixed effects that contributed

significantly to the model. In all animal models, we included random effects representing the identity of the hyena, the identity of the hyena's mother, and a term representing the additive genetic effect in order to estimate the desired parameters of each model. For the aggression intensity models, we also included a random effect of the session identifier.

Because MCMCglmm requires values for all random effects, we generated unique maternal identities for immigrant males and natal animals born before our study began, following Taylor et al. (2012). This technique allows for the estimation of maternal effects, even when pedigree information is missing; however, it assumes that all hyenas with unknown maternity are unrelated.

For each measure of aggressiveness, we calculated heritability, maternal effects, and permanent environment effects by dividing the relevant variance component by the total phenotypic variance. Following Lessels and Boag (1987), we calculated repeatability by dividing the among-individual variance by the total among- and within-individual variance.

The posterior distribution of the animal model was sampled every 500 iterations after a burn-in period of 20,000 iterations for a total of 5,000 samples.

Stability over time and across aggression contexts

To assess whether the aggressiveness of individual hyenas remained stable over time, we created generalized linear mixed models using the lme4 function in R. To compare aggressive behavior early in life to that later in life, we included only aggressive acts emitted when the aggressor was either a cub (less than 12 months of age) or an adult (more than 24 months of age). For cubs, we included all aggressive acts, and for adults we included only

aggressive acts directed at adults but not in the presence of food; this way, we could assess whether the general level of aggressiveness early in life predicted a more specialized type of aggressive behavior during adulthood. Only hyenas observed to emit at least two aggressive acts during each age interval (cub and adult) were included in this analysis.

In these models, we used aggression intensity as the response variable and age class as the main fixed effect of interest. The sex, standardized social rank and age of the aggressor and the proportion of targets in the session were also included as fixed effects. Only fixed effects that lowered the Akaike information criterion (AIC) value of the model were retained in the final model. A unique session identifier was included as a random effect in all models to control for pseudoreplication.

We included individual as a random intercept to allow for the variation in aggressiveness between hyenas, as suggested by earlier analyses. We also added a random slope to the model, which described the extent to which the aggressiveness of individual hyenas changed across ontogeny. If this term significantly improved the fit of the model, we concluded that aggressiveness in hyenas was not a trait that changed consistently among individuals across age classes. To test the significance of this term, we created two models that were identical except for the inclusion of the random slope. We then compared these two models with a log-likelihood ratio test, in which the log-likelihood ratio was calculated as $2[\log\text{-likelihood of model B} - \log\text{-likelihood of model A}]$, and tested as a chi-squared distribution (Pinheiro & Bates 2000; Martin & Réale 2008). The approach of using random regression to investigate behavioral reaction norms is described in more detail in Dingemanse et al. (2010).

Using the same methodology, we ran a set of similar models to test whether the aggressiveness exhibited by individual hyenas was context-specific or domain-general. If aggressiveness in hyenas is context-specific, hyenas that are relatively aggressive over food should also be more aggressive than other hyenas in non-food contexts. In these models, we used aggression context (either “food” or “non-food”) as the main fixed effect of interest, and defined the random slope to allow the aggression intensity of an individual to differ across contexts. Only adult female hyenas with at least 50 FAs and 50 NFAs were included in this analysis.

Relationship between aggressiveness and fitness

Finally, we tested whether a hyena’s aggressiveness was related to its fitness, as indicated by various measures of reproductive success. For these analyses, we used NFA and FA lifetime aggression rates as our measures of aggressiveness. The only hyenas included in this analysis were females that were born after our study began, died before our study ended, and were present in at least 50 sessions with potential targets for FAs and at least 50 sessions with potential targets for NFAs.

As indicators of reproductive success, we used the total number of cubs borne by each female over her lifetime, as well as the proportion of her cubs that survived to three life-history milestones: den independence, weaning, and reproductive maturity (24 months of age). We created two sets of linear and second-order polynomial models with these fitness components as the response variables, and maternal rank and either lifetime FA rate or lifetime NFA rate as

predictors, as well as an interaction term between the lifetime aggression rate and maternal rank. All variables in these analyses were Z-transformed.

We also assessed whether lifetime aggression rates of females were related to the amount of time their offspring spent feeding at kills. For this analysis, we included only offspring younger than 36 months of age, because until this age, hyenas are at a developmental feeding disadvantage (Watts & Holekamp 2009; Tanner et al. 2010). For all sessions in which hyenas less than 36 months of age with known mothers were observed at carcasses or kills with conspecifics, we calculated the number of minutes these young hyenas fed, based on behavioral scan data. Scans were conducted, when possible, at regular 15-minute intervals. We created an MCMCglmm model predicting the number of minutes the hyena fed, and included as fixed effects the total number of scans (i.e. the potential minutes during which the hyena could have been observed feeding), the sex and age of the hyena, its standardized rank in the session, the total number of hyenas present, the proportion of higher-ranking hyenas present, whether or not the cub's mother was present in the session, and the estimated size category of the prey (less than 100 kg, between 100 kg and 200 kg, between 200 kg and 500 kg, or more than 500 kg). A random effect representing the session identifier was included to control for pseudoreplication.

First, we added, and tested the significance of, a random effect representing the identity of the mother to determine whether her identity affected the feeding success of her offspring in some way. Then, we removed the random effect of maternal identity and added a fixed effect representing the lifetime aggression rate of the mother. We created two similar models, one with her lifetime NFA rate and one with her lifetime FA rate. Significance of either of these

terms would suggest that the aggressiveness of female hyenas can affect the feeding success of their offspring. In this analysis, we only included the offspring of mothers that were present in at least 50 sessions with potential targets for FAs, and in at least 50 sessions with potential targets for NFAs.

RESULTS

Social and environmental factors influencing aggressiveness

Aggression count

There were 8126 sessions that met our criteria for the FA count analysis. On average, there were 0.529 ± 0.02 FAs per session and in 6738 (82.9%) of these sessions, hyenas did not emit aggressions in the context of food. Hyenas emitted more FAs in longer sessions than shorter sessions, in sessions with fewer hyenas present than those with more hyenas present, and in sessions between noon and midnight, compared to sessions earlier in the day (Appendix, Table 3.A1). The FA count in each session was higher during seasons of low prey availability than during seasons of high prey availability, and there were more FAs at fresh kills than dens, but fewer FAs at old carcasses than at dens (Appendix, Table 3.A1).

In the same time frame, there were 14735 sessions that met our criteria for inclusion in the NFA count analysis. On average, there were 0.637 ± 0.016 NFAs per session; hyenas did not emit any NFAs in 10766 (73.1%) of these sessions. The mean NFA count was significantly greater than the mean FA count (Kruskal-Wallis: $H=238.561$, $df=1$, $p<0.001$). There were more NFAs when seasonal prey availability was low than when it was high, and more NFAs at kills, dens, and at mating events than at other locations (Appendix, Table 3.A2). NFA counts were

higher in longer than shorter sessions, and higher in sessions with more hyenas present than in those with fewer hyenas (Appendix, Table 3.A2).

Aggression intensity

Between 1988 and 2009, there were 859 sessions with FAs that met our criteria for inclusion in the intensity analysis; the average intensity of these FAs was 1.84 ± 0.02 . During this time, there were 3038 sessions with NFAs that met our criteria for inclusion in this analysis. The intensity of the NFAs in these sessions averaged 1.59 ± 0.01 . Average FA intensities were significantly greater than mean NFA intensities (Kruskal-Wallis: $H=133.818$, $df=1$, $p<0.001$).

Intensities of both FAs and NFAs were greater between noon and midnight than earlier in the day (Appendix, Tables 3.A3 and 3.A4). NFAs emitted at dens and during mating events were more intense than those emitted at other locations (Appendix, Table 3.A4). The intensities of FAs did not differ significantly between dens and fresh kills, but FAs emitted at old carcasses were less intense than those emitted at dens (Appendix, Table 3.A3). NFA intensity increased as the number of hyenas present increased, and there was a similar, but non-significant, trend for FA intensity to increase as the number of hyenas present increased (Appendix, Tables 3.A3 and 3.A4).

Consistency in aggressiveness within individuals

Aggression count

There was no evidence for consistency within individuals in either FA or NFA counts; including a random effect of the identity of the aggressor did not improve model fit (food:

DIC=14528.05; non-food, DIC=26035.88) over models that did not include this random effect (food: DIC=12172.34; non-food, DIC=27319.11).

Both FA and NFA counts increased as the proportion of lower-ranking hyenas in the session increased (Appendix, Tables 3.A5 and 3.A6). Older females emitted more NFAs than did younger females, higher-ranking hyenas emitted more NFAs than did lower-ranking hyenas, and females emitted more NFAs than did males (Appendix, Table 3.A6).

Aggression intensity

For aggression intensity, including a random effect of the identity of the aggressor significantly improved the model for each aggression context in both sexes (Table 3.1), suggesting that there are consistent inter-individual differences in the intensity of FAs and NFAs emitted by both male and female hyenas.

Table 3.1

DIC values yielded by separate MCMCglmm models run with NFAs and FAs emitted by adults (≥ 24 months of age) of each sex. DIC values are given for models with only a random effect of the session identifier, and for models run with both a session identifier and an aggressor identifier. For each context in each sex, the better model is marked with an asterisk.

Sex and aggression context	Random effects included	
	Session	Aggressor and Session
Females, non-food	8311.299	8248.891*
Females, food	5274.435	5242.795*
Males, non-food	1091.263	1065.257*
Males, food	1232.201	1223.305*

Younger females emitted higher-intensity NFAs than did older females, but age had no effect on the intensity of FAs emitted by females (Appendix, Tables 3.A7 and 3.A8). FAs emitted by females were of higher intensity when there was a greater proportion of lower-ranking

hyenas present than when there were fewer lower-ranking hyenas present (Appendix, Table 3.A7). No fixed effects significantly predicted the intensity of either FAs or NFAs emitted by males; however, in each context, there was a non-significant trend for intensity to increase as the proportion of lower-ranking hyenas increased (Appendix, Tables 3.A9 and 3.A10)

Heritability of aggressiveness

Lifetime aggression rate

For lifetime FA rates, both heritability and maternal effects were significant, as indicated by a lower DIC value when these effects were included in a model, compared to when they were omitted (Appendix, Table 3.A11). The heritability estimate from the MCMCglmm animal model for lifetime FA rates was 0.260 (95% CI=0.093 to 0.593, Figure 3.1) and the maternal effect estimate was 0.128 (95%CI=0.059 to 0.277, Figure 3.1).

In terms of lifetime NFA rates, both heritability and maternal effects were significant, as indicated by a lower DIC value when these effects were included in a model, compared to when they were omitted (Appendix, Table 3.A11). The heritability estimate from the MCMCglmm animal model for lifetime NFA rate was 0.320 (95% CI=0.065 to 0.590, Figure 3.1), and the maternal effect estimate was 0.291 (95%CI=0.079 to 0.543, Figure 3.1).

Aggression intensity

Animal model estimates for aggression intensities were much lower than animal model estimates for lifetime aggression rates, and in some cases were non-significant. In terms of FA intensity, heritability, maternal effects, and permanent environment effects were significant, as indicated by a lower DIC value when these effects were included in a model, compared to when

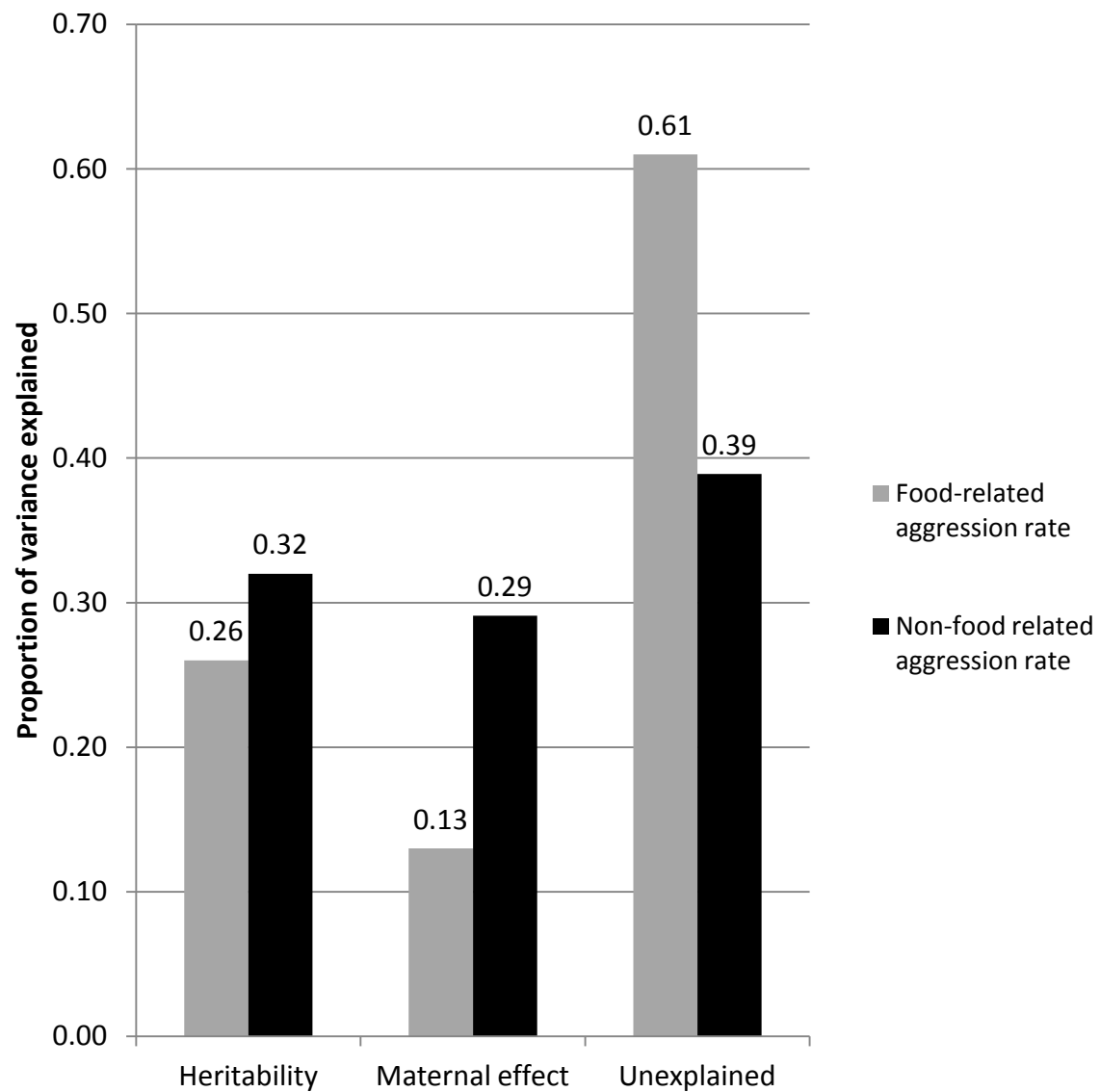


Figure 3.1. The percent of variation in lifetime food-related and non-food aggression rates attributable to heritability and maternal effects, and the remaining unexplained variation. Variances were estimated with MCMCglmm animal models.

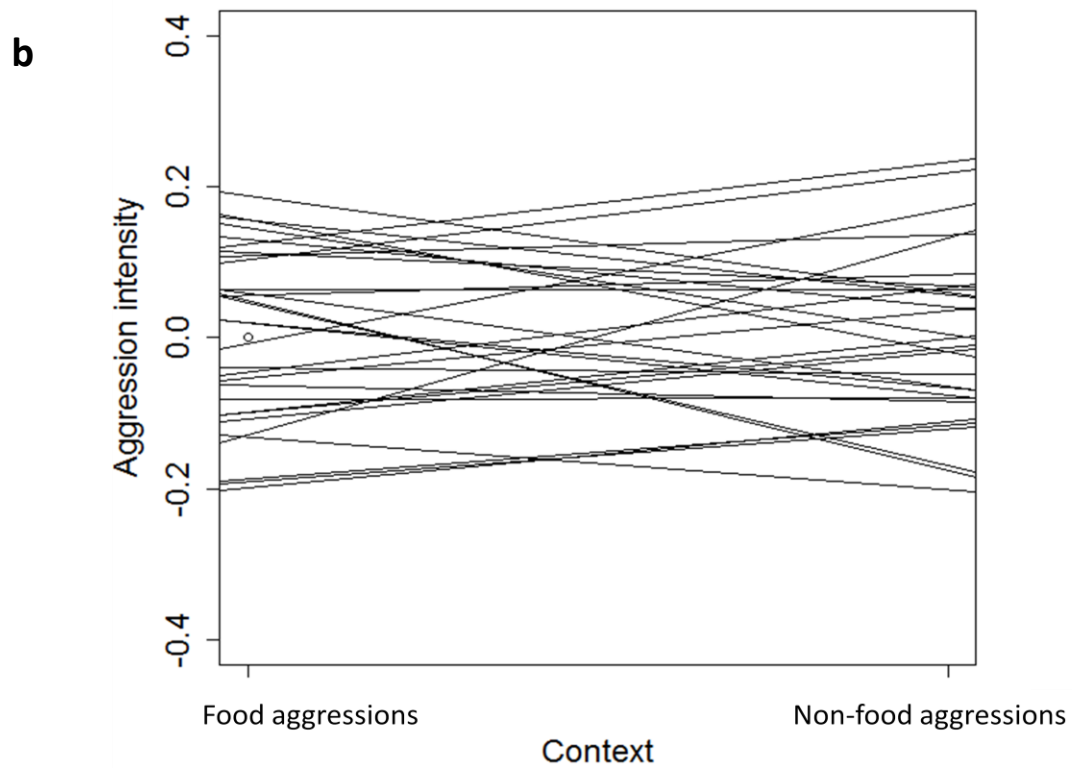
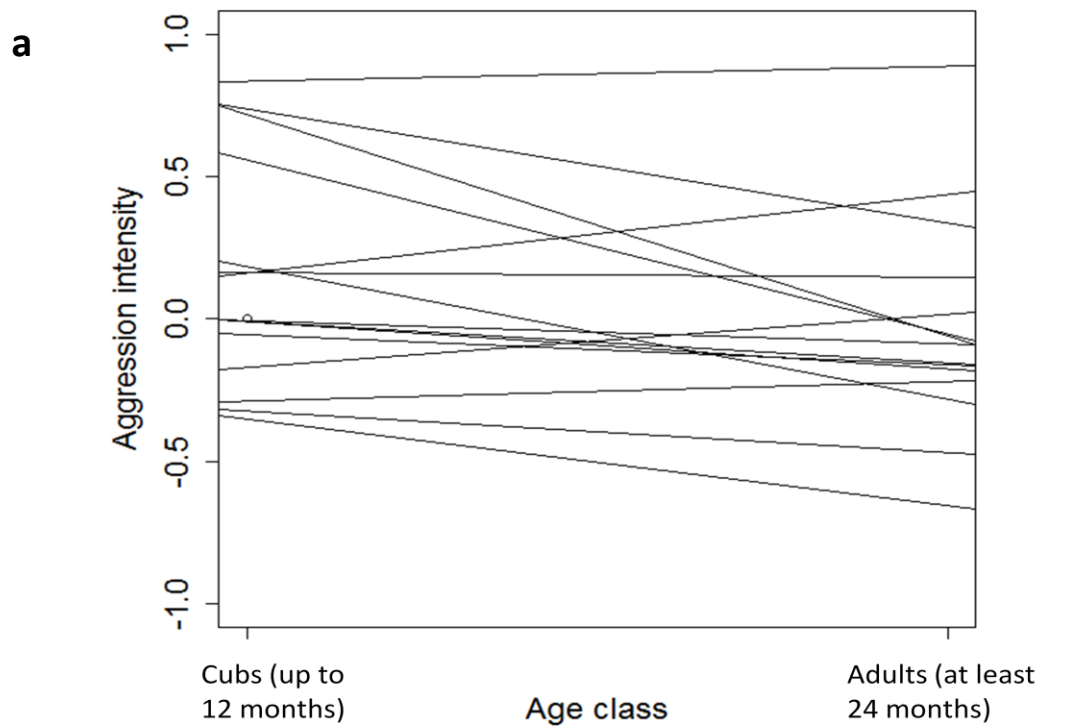
they were omitted (Appendix, Table 3.A11). The heritability estimate from the MCMCglmm animal model for FA intensity was 0.042 (95% CI= 2.506×10^{-5} to 0.102), the permanent environment effect was 1.181×10^{-4} (95% CI= 7.011×10^{-11} to 0.065), and the maternal effect estimate was 6.969×10^{-5} (95% CI= 1.587×10^{-10} to 0.0602).

For NFA intensity, heritability and maternal effects were significant, as indicated by a lower DIC value when these effects were included in a model, compared to when they were omitted (Appendix, Table 3.A11). Permanent environment effects for this trait were not significant (Appendix, Table 3.A11). For NFA intensity, the heritability estimate was 0.026 (95% CI=0.003 to 0.080) and the maternal effect estimate was 0.044 (95% CI= 5.299×10^{-4} to 0.116).

The estimate for the repeatability of FA intensity was 0.067 (95% CI=0.013 to 0.126), and the estimate for the repeatability of NFA intensity was 0.0263 (95% CI=0.003 to 0.080). These repeatability values suggest that aggression intensity in each context is significantly repeatable, but there is still a great amount of within-individual variation in this measure.

Stability over time and across contexts

Fifteen female hyenas met our criteria for inclusion in the age class analysis. The model including a random slope of age class in addition to the random intercept was not significantly better at predicting the aggressiveness of individuals than the model with only the random intercept (LRT=2.199, df=2, p=0.333, Figure 3.2a). The inclusion of a random slope in this model was not significant, indicating that the intensities of aggressions emitted by individual hyenas generally change in a consistent way across ontogeny.



Figures 3.2a and 3.2b. Predicted behavioral reaction norms for aggression intensity across (a) two age classes and (b) two aggression contexts. Each line represents how the behavior of an individual changes across categories.

Thirty one females met our criteria for inclusion in the context analysis. For this analysis, including a random slope of aggression context did improve the fit of the model (LRT=-9.076, df=2, p=0.011, Figure 3.2b). The inclusion of a random slope was significant, indicating that the aggression intensity in hyenas is context-specific, rather than domain-general.

Relationship between aggressiveness and fitness

Aggression intensity

Thirty-one females met the criteria for our analysis of the relationship between aggression intensity and fitness. Generalized linear models and second-order polynomial models showed no relationship between either FA or NFA intensity and any measure of reproductive success, and there were no significant interactions between reproductive success and aggression intensity ($p > 0.1$).

Lifetime aggression rate

Thirty-two females satisfied the criteria for inclusion in our analysis of the relationship between aggression rate and reproductive success. We found that the lifetime NFA rate of a female is significantly related to the proportion of her cubs that survive to 24 months of age; the offspring of females with higher lifetime NFA rates are more likely to survive to reproductive maturity than the offspring of other females (0.719 ± 0.300 , $t = 2.401$, $p = 0.025$). There was a similar, although non-significant, relationship between a female's lifetime NFA rate and the proportion of her cubs that survive to weaning (0.512 ± 0.296 , $t = 1.733$, $p = 0.096$).

We did not find any direct relationship between any measure of reproductive success and lifetime FA rate ($p > 0.1$). However, we found several significant interactions between

lifetime FA rate and maternal rank. Whereas high-ranking hyenas had consistently high reproductive success regardless of their lifetime aggression rates, low-ranking females with high lifetime FA rates had better reproductive success than low-ranking females that were less aggressive in feeding contexts. This interaction was significant for the proportion of cubs surviving to weaning (0.690 ± 0.253 , $t=2.725$, $p=0.012$) and the proportion of cubs surviving to reproductive maturity (0.651 ± 0.269 , $t=2.416$, $p=0.024$). No second-order polynomial terms were significant predictors of reproductive success, and second-order polynomial models were not significantly better than linear models at predicting the reproductive success of females ($p>0.1$).

In our analysis of time spent feeding at kills, we found that maternal identity was an important predictor of offspring feeding time at kills, even after controlling for social rank and the presence of higher-ranking hyenas. Including a random effect of maternal identity improved the model ($\text{DIC}=6713.464$), compared to one without maternal identity ($\text{DIC}=6735.044$). Furthermore, after removing the maternal identity term from the model, the lifetime FA rate of the mother was a significant predictor of offspring feeding time; the offspring of mothers with higher lifetime FA rates fed longer among conspecifics at kills than did the offspring of mothers with lower lifetime FA rates (0.846 , $95\% \text{ CI}=-0.028$ to 1.571 , $p=0.05$). The lifetime NFA rate of the mother was not a significant predictor of offspring feeding time ($p=0.775$).

DISCUSSION

Overall, our analyses show that there are consistent inter-individual differences among spotted hyenas in some measures of aggressiveness, and that aggressiveness has significant implications for the reproductive success of females. We found that males and females are consistent in the intensity of their aggressive behavior, both in the context of food and in situations unrelated to food. However, we did not find that the number of aggressive acts emitted by hyenas in either context were consistent across repeated observations.

For both food and non-food-related aggression contexts, the location of the observation session and several other situational variables were highly significant predictors of both the number and intensity of aggressive acts observed. The number of FAs and the number and intensity of NFAs increased with the number of hyenas present in the session. Hyenas tended to emit more food-related and non-food-related aggressions during seasons when prey availability was low, compared to seasons where food was more abundant. However, aggression intensity was not related to seasonal prey availability.

At the level of individual, adults emitted more food-related and non-food-related aggressions as the proportion of lower-ranking hyenas in a session increased, indicating that hyenas generally become more aggressive when more targets of aggression are present. Males emitted fewer aggressions than females did in non-food contexts, but not in food-related contexts, which supports a similar finding by Van Meter (2009) that the rates of intra-sexual aggression over food did not differ between the sexes. None of our individual-level predictor variables were significant predictors of the intensity of aggressive acts emitted by males, indicating that male aggressiveness may be more strongly driven by the situational variables

and personality traits than by individual attributes at the time of the session, such as age or social rank.

Among spotted hyenas, aggression intensity appears to be context-specific; that is, hyenas that emitted particularly intense aggressions over food did not necessarily also emit intense aggressions in contexts away from food. This resembles findings in humans (e.g. Kagan 2003), and suggests that food-related and non-food-related aggression emitted by hyenas likely have very different functions, and that the mechanisms mediating these two types of aggressions may differ.

Unlike aggression intensity, which was consistent for both males and females across repeated observations, we found that aggression counts for individual hyenas were not consistent across sessions. The number of aggressions exhibited by a hyena in a session may be strongly driven by the situational aspects of the session included in our analyses, as well as others that we could not account for. For instance, group composition is an important determinant of whether or not hyenas attack each other (Smith et al. 2010); whereas we were able to control for the proportion of lower-ranking hyenas present in our analyses, we could not control for the presence of specific hyenas that may have incited or suppressed aggression, or for combinations of individuals that may have been particularly volatile. Moreover, especially in regard to food-related aggression, motivational state is likely to vary between sessions and drive aggressive behavior (Stocker & Huber 2001; Hodge et al. 2009).

When aggression counts were averaged over time in our lifetime aggression rate measure, there were significant heritable differences among individuals, and aggressive behavior was subject to significant maternal effects. As noted previously, differences between

heritability and maternal effect estimates were due to sire effects within dams. The average heritability of behavioral traits is 0.30 ± 0.02 (Mousseau & Roff 1987), and our heritability estimates for aggressiveness in both contexts were close to this average. Our maternal effect estimate for lifetime non-food aggression rate was quite substantial; roughly a third of the variation in this type of aggressive behavior could be explained by maternal effects. The maternal effect estimate for food-related aggression rate was lower, but still larger than maternal effect estimates for aggressive behavior in some other free-living mammals (e.g. Taylor et al., 2012), indicating that maternal effects play a substantial role in multiple types of aggressive behavior in hyenas. This is consistent with earlier findings by Dloniak et al. (2006) and Van Meter (2009), who found significant correlations between circulating maternal fecal androgen levels during gestation and the aggression rates exhibited by offspring. Our significant heritability and maternal effect estimates for lifetime aggression rates, along with our finding that aggression intensity was stable across age classes, suggest that some aspects of aggressive behavior are determined very early in life.

Interestingly, for aggression intensity, our estimates for heritability, maternal effects, and permanent environment effects were extremely small, despite evidence of consistent differences across observation sessions. Again, subtle or unmeasurable differences between sessions may have contributed to these very low estimates. Our low repeatability estimates for these measures suggest that, although individual differences in aggression intensity are statistically consistent across observation sessions, there is still much within-individual variation across repeated observations in this measure of aggressiveness. Differences in aggressiveness may be difficult to observe in hyenas on a session-by-session basis in the wild. However, over

time, inter-individual differences in aggression in this species become evident and have significant implications for fitness.

When we used lifetime aggression rates to predict the reproductive success of females, we found that the offspring of females with high non-food aggression rates enjoyed better survival than did offspring of females that are less aggressive in non-food situations. Mortality rates are high before 2 years of age (Watts & Holekamp 2009), and maternal interventions and other aggressive behaviors that are emitted outside the context of food likely play an important role in defending and protecting offspring during vulnerable life history stages. Furthermore, we found a significant interaction between lifetime food-related aggression rate and maternal rank, indicating that frequent food-related aggressions emitted by an adult female may increase the likelihood that her cubs will survive to weaning and reproductive maturity, and that this beneficial effect of aggressiveness increased as rank decreased. Hyenas that are particularly aggressive over food are likely to displace conspecifics from kills more often, thereby increasing their own ability to feed. Reproductive success is determined by access to resources among female hyenas (Holekamp & Smale 1996), and it appears that females can enhance their reproductive success by increasing their food intake. The advantages accruing from food-related aggression increased as rank decreased, indicating that better access to food may be particularly beneficial for lower-ranking individuals. Holekamp and Smale (1996) suggested that high-ranking female hyenas were buffered from the consequences of fluctuating prey availability due to their priority access to resources; a similar effect may be at work here, as increased aggression over food may not benefit higher-ranking females as much as it does lower-ranking females.

The results of our offspring feeding time analysis suggest that increased tolerance of a female's offspring at kills may be a benefit of high rates of food-related aggression emitted by mothers. We found that the offspring of females that were particularly aggressive over food were able to feed longer among conspecifics than could the offspring of females that were less aggressive over food. Our results suggest that hyenas up to 36 months of age may benefit in this way from having more aggressive mothers. Until about three years of age, young hyenas are at a competitive disadvantage during group feeding events because their skulls and feeding apparatuses have not yet finished developing (Watts et al. 2009; Tanner et al. 2010). It is thought that this protracted developmental period, in tandem with the intense feeding competition seen in hyena clans, favored the evolution of large, aggressive females (Watts et al. 2009). Our results suggest that female aggressiveness in food-related contexts might mitigate this competitive disadvantage for offspring. The rather unusual set of constraints imposed by slow morphological development and intense feeding competition may be the reason that aggressiveness has a positive effect on reproductive success in hyenas, whereas high levels of aggression decrease some aspects of fitness in other species (e.g. Packer et al. 1995; Duckworth 2006).

Further studies investigating individual differences in both food-related and non-food aggression should inform our understanding of the effects of aggressiveness on fitness, as well as the interaction between rank and aggressiveness. Although we have shown here that rank-independent differences in aggressiveness among hyenas drive some variation in reproductive success, social rank is still the most important predictor of reproductive success (Holekamp & Smale 1996; Swanson et al. 2011). Interestingly, we see definite differences in the fitness

benefits of aggressiveness for low- and high-ranking hyenas. We hypothesize that these differences are due to the effect of rank on resource acquisition; whereas high-ranking females are always able to displace conspecifics from kills, increased aggressiveness may improve the resource holding potential of lower-ranking females to a greater degree. Future studies focusing on the behavior of individuals at group feeding events may be able to clarify the relationship between aggression rate, food intake, and social rank. For instance, it is currently unknown whether a high aggression rate at a kill directly increases the time an individual spends feeding in that session, and whether this effect varies with social rank. Alternatively, it is possible that a “history” of frequent aggressions over food is enough to increase an individual’s food consumption at a kill. Additionally, although we did not find a negative relationship between aggressiveness and reproductive success, it is possible that high rates of aggression may have associated costs in other areas. For example, in some species, individuals prone to aggressive behavior experience increased metabolic demands (e.g. Matsumasa & Murai 2005) and injury rates (e.g. Wilson & Boelkins 1970) compared to less aggressive individuals; it is not yet clear whether high levels of aggression have similar consequences for hyenas.

APPENDIX

Table 3.A1

Fixed effects predicting the total FA count in each session. Only aggressive acts directed by adults (≥ 24 months of age) down the hierarchy toward other adults are included. Significant fixed effects are marked with asterisks.

	Posterior mode	95% credible interval	p _{MCMC}
<i>Poisson</i>			
(Intercept)	2.2977	(2.01705 to 2.58161)	<0.001*
Location (carcass)	-4.37379	(-4.87854 to -3.78269)	<0.001*
Location (kill)	3.11857	(2.85094 to 3.36689)	<0.001*
Time of day (PM)	0.47438	(0.31709 to 0.65134)	<0.001*
Number of hyenas present	0.03666	(0.02439 to 0.04805)	<0.001*
Session length	0.74779	(0.59287 to 0.91887)	<0.001*
Prey availability (low)	0.19324	(0.01666 to 0.38226)	0.0389*
<i>Zero-inflated</i>			
(Intercept)	1.21186	(0.96698 to 1.45397)	<0.001*
Session length	-0.54217	(-0.67857 to -0.3971)	<0.001*
Prey availability (low)	0.26127	(-0.04531 to 0.65901)	0.1306

Table 3.A2

Fixed effects predicting the total NFA count in each session. Only aggressive acts directed by adults (≥ 24 months of age) down the hierarchy toward other adults are included. Significant fixed effects are marked with asterisks.

	Posterior mode	95% credible interval	p _{MCMC}
<i>Poisson</i>			
(Intercept)	-2.693988	(-2.911986 to -2.48687)	<0.001*
Location (den)	0.503852	(0.385957 to 0.621126)	<0.001*
Location (kill)	0.209515	(0.054158 to 0.361203)	0.008*
Location (mating)	1.338414	(1.100465 to 1.568188)	<0.001*
Location (carcass)	0.181835	(-0.132920 to 0.491380)	0.261
Time of day (PM)	-0.004432	(-0.095446 to 0.090116)	0.903
Number of hyenas present	0.056039	(0.048147 to 0.064742)	<0.001*
Session length	0.277183	(0.190224 to 0.360318)	<0.001*
Prey availability (low)	0.142071	(0.049520 to 0.240325)	0.002*
<i>Zero-inflated</i>			
(Intercept)	3.478454	(2.769206 to 3.978756)	<0.001*
Session length	-8.504293	(-9.676932 to -5.820411)	<0.001*

Table 3.A3

Fixed effects predicting the average FA intensity in each session. Only aggressions directed by adults (≥ 24 months of age) down the hierarchy to other adults are included. Significant fixed effects are marked with asterisks.

	Posterior mode	95% credible interval	p_{MCMC}
(Intercept)	1.816063	(1.692739 to 1.999028)	<0.01*
Location (carcass)	-0.2376	(-0.476201 to -0.059231)	<0.01*
Location (kill)	0.059606	(-0.162098 to 0.038545)	0.38
Number of hyenas present	0.004783	(-0.001109 to 0.008981)	0.08
Time of day (PM)	0.113481	(0.031890 to 0.212463)	0.04*
Prey availability (low)	0.031494	(-0.050913 to 0.102473)	0.38

Table 3.A4

Fixed effects predicting the average NFA intensity in each session. Only aggressions directed by adults (≥ 24 months of age) down the hierarchy to other adults are included. Significant fixed effects are marked with asterisks.

	Posterior mode	95% credible interval	p_{MCMC}
(Intercept)	1.4610220	(1.343075 to 1.545208)	<0.01*
Location (den)	0.126464	(0.069829 to 0.177375)	<0.01*
Location (kill)	0.081427	(0.022554 to 0.158401)	0.06
Location (mating)	0.155056	(0.076016 to 0.238748)	<0.01*
Location (carcass)	0.065156	(-0.035453 to 0.165568)	0.16
Number of hyenas present	0.005805	(0.002295 to 0.009367)	<0.01*
Time of day (PM)	0.061963	(0.019212 to 0.101909)	<0.01*
Prey availability (low)	-0.034516	(-0.073343 to 0.002779)	0.16

Table 3.A5

Fixed effects predicting the FA count by each hyena in each session. Only aggressions directed by adults (≥ 24 months of age) down the hierarchy to other adults are included, and all sessions that were shorter than 30 minutes or had no aggressions were omitted. Significant fixed effects are marked with asterisks.

	Posterior mode	95% credible interval	p _{MCMC}
<i>Poisson</i>			
(Intercept)	-8.3263814	(-9.7106529 to -6.3727372)	<0.001*
Sex (male)	-0.1566183	(-0.4255145 to 0.1454277)	0.292
Age	0.0007395	(-0.0017825 to 0.0032776)	0.58
Standardized rank	0.9155038	(-0.3683651 to 2.1918252)	0.148
Proportion of targets	5.2782115	(3.5488414 to 6.9030409)	<0.001*
<i>Zero-inflated</i>			
(Intercept)	-6.1499061	(-7.6089937 to -4.0470538)	<0.001*
Age	0.0084016	(0.0032528 to 0.0142680)	<0.001*

Table 3.A6

Fixed effects predicting the NFA count by each hyena in each session. Only aggressions directed by adults (≥ 24 months of age) down the hierarchy to other adults are included, and all sessions that were shorter than 30 minutes or had no aggressions were omitted. Significant fixed effects are marked with asterisks.

	Posterior mode	95% credible interval	p _{MCMC}
<i>Poisson</i>			
(Intercept)	-3.136161	(-3.614926 to -2.712158)	<0.001*
Sex (male)	-0.904921	(-1.157348 to -0.672857)	<0.001*
Age	0.005109	(0.002837 to 0.007353)	<0.001*
Standardized rank	-0.936564	(-1.490512 to -0.344600)	<0.001*
Proportion of targets	1.615436	(1.117032 to 2.200340)	<0.001*
<i>Zero-inflated</i>			
(Intercept)	-3.312539	(-3.921171 to -2.83293)	<0.001*
Age	0.014052	(0.010708 to 0.017718)	<0.001*

Table 3.A7

Fixed effects predicting the intensity of FAs emitted by adult (≥ 24 months of age) females.
Significant effects are marked with asterisks.

	Posterior mode	95% credible interval	p_{MCMC}
(Intercept)	0.5053389	(-0.0403970 to 1.0255745)	0.06*
Age	0.0014929	(-0.0037310 to 0.0005699)	0.19
Standardized rank	-0.5000345	(-1.1307486 to 0.0232113)	0.08
Proportion of targets	0.7582205	(0.1616710 to 1.3726560)	0.005*

Table 3.A8

Fixed effects predicting the intensity of NFAs emitted by adult (≥ 24 months of age) females.
Significant effects are marked with asterisks.

	Posterior mode	95% credible interval	p_{MCMC}
(Intercept)	0.5386560	(0.129524 to 0.978908)	0.005*
Age	-0.0035970	(-0.006204 to -0.001508)	<0.003*
Standardized rank	-0.1021480	(-0.585966 to 0.420753)	0.68
Proportion of targets	-0.3603050	(-0.798148 to 0.125683)	0.115

Table 3.A9

Fixed effects predicting the intensity of FAs emitted by adult (≥ 24 months of age) males.
Significant effects are marked with asterisks.

	Posterior mode	95% credible interval	p_{MCMC}
(Intercept)	-0.12736	(-1.008385 to 0.960142)	0.77
Age	0.004635	(-0.002327 to 0.010014)	0.16
Standardized rank	-1.111081	(-2.596731 to 0.143540)	0.1
Proportion of targets	1.140719	(-0.095912 to 2.161934)	0.06

Table 3.A10

Fixed effects predicting the intensity of NFAs emitted by adult (≥ 24 months of age) males.
Significant effects are marked with asterisks.

	Posterior mode	95% credible interval	p_{MCMC}
(Intercept)	-0.9926710	(-1.991511 to -0.007707)	0.05*
Age	0.0013020	(-0.004247 to 0.006771)	0.665
Standardized rank	0.8906690	(-0.427330 to 2.260357)	0.16
Proportion of targets	1.2727010	(-0.159216 to 2.508053)	0.065

Table 3.A11

DIC values yielded by separate MCMCglmm models predicting adult (≥ 24 months of age) lifetime aggression rate and aggression intensity for each aggression context. DIC values are given for the full model with all variance components including V_A (additive genetic), V_M (maternal effect), and V_I (permanent environment effect), as well as for models omitting each variance component. Relevant fixed effects were retained in each model, and intensity models also include a random term representing the session identifier.

		Models with omitted effects			
	Context	Full model	V_A omitted	V_M omitted	V_I omitted
Lifetime aggression rate	Food	-403.452	-382.919	-400.942	NA
Lifetime aggression rate	Non-food	-435.156	-420.296	-407.336	NA
Aggression intensity	Food	6101.237	6104.711	6110.397	6103.556
Aggression intensity	Non-food	13613.51	13619.19	13623.31	13605.48

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CHAPTER 4

INDIVIDUAL DIFFERENCES IN SOCIABILITY AMONG SPOTTED HYENAS

INTRODUCTION

Sociality has evolved multiple times in species representing very diverse taxa, and gregariousness can be advantageous in many ways, including cooperative defense of resources, group acquisition of food, and enhanced vigilance (O'Brien 1991; Baker et al. 1998; Hass & Valenzuela 2002; Baglione et al. 2002; Majolo et al. 2008). On an individual level, animals living in groups may also benefit from associations with conspecifics through mechanisms like coalitionary support, cooperative breeding, and social learning (Coussi-Korbel & Fragasz 1995; Clutton-Brock 2002; Silk et al. 2004). In gregarious species, group members may differ from one another with respect to how often they engage in social behavior, or in the strength of their associations with conspecifics. Sociability is the extent to which an individual engages in social behavior; Reale et al. (2007) described sociable individuals as those that "seek the presence of conspecifics, while unsociable individuals avoid conspecifics." As studies of animal personality become more common, researchers are finding that this inter-individual variation in sociability is often consistent over time, and that it can have significant effects on fitness (e.g. Wilson et al. 1994; Reale & Festa-Bianchet 2003; Carere et al. 2005; Boon et al. 2008; Smith & Blumstein 2008). Whereas traits such as aggression, exploratory behavior, and activity have received a substantial amount of attention, sociability is one of the least-studied personality traits in non-human animals (however, see Armitage 1986; Capitanio 2002; Silk et al. 2006).

Consistent inter-individual variation in sociability has been reported in several species, including sticklebacks (Dingemanse et al. 2009), yellow-bellied marmots (Barash 1976; Armitage 1986), zebra finches (Figueredo et al. 1995), domestic dogs (Svartberg & Forkman 2002), rhesus macaques (Capitanio 2002; Maninger et al. 2003), and humans (Goldsmith & Gottesman 1981; Loehlin 1992). Research on common lizards suggests that sociability is stable across ontogeny; in these studies, the social behavior of juvenile lizards did not change significantly as they reached reproductive maturity (Cote & Clobert 2007; Cote et al. 2008). However, in a study of wolf cubs, Macdonald (1983) found that the ontogenetic development of sociability and other personality traits varied greatly among individuals. Some cubs changed their behavior in drastically different ways in early development, and the behavior of others remained relatively stable. In humans and other primates, early experience, such as interactions with kin or members of a peer cohort, is hypothesized to shape sociability later in life (Capitanio 1999; Fries et al. 2005).

Some studies point to genetics as a major source of variability in sociability (e.g. Haas et al. 2009). Researchers have successfully selected for strains of mice that show particularly high or low rates of social interaction (Sankoorikal et al. 2006; Brodtkin 2007). A heritability estimate is the proportion of the phenotypic variance that can be accounted for by genetics; for humans, the heritability of sociability has been estimated at between 0.25 and 0.4 (Plomin 1994). Similarly, Wilsson and Sundgren (1997) estimated that just over one third of the variation in social behavior among German Shepherds could be explained by genetic effects. As sociability is one of the less well-studied personality traits in non-human animals, heritability estimates for this trait in species other than humans and domestic dogs are rare.

The effects of sociability on fitness have received more attention than other aspects of sociability. Cote et al. (2008) found that, among common lizards, higher levels of sociability increased the reproductive success of females, but not males. In these lizards, sociability also influenced dispersal decisions; individuals with greater social tolerance tended to disperse to higher-density populations, whereas those with less social tolerance dispersed toward lower-density populations (Cote & Clobert 2007). Silk et al. (2003) demonstrated that the offspring of female baboons that rated highly on a composite sociality index were more likely to survive than the offspring of females that were less social, even when controlling for the effects of dominance rank. Female baboons that form stronger and more stable bonds also live longer than do less social females (Silk et al. 2010). It is suggested that sociability enhances fitness via increased protection from harassment, better cooperative relationships with partners, and more frequent interactions with potential mates (Armitage 1986; Silk et al. 2003; Cote et al. 2008; Schulke et al. 2010)

Here, we study sociability in a social carnivore, the spotted hyena (*Crocuta crocuta*). Hyenas are among the most gregarious large carnivores, living in groups containing up to 90 individuals (Holekamp et al. 2006). These groups are fission-fusion societies, where group members are seldom, if ever, all together. Instead, smaller subgroups form (“fission”) and break apart (“fusion”), and these subgroups vary in size and composition over time (Kummer 1971; Smith et al. 2008). Various social and environmental factors contribute to fission-fusion dynamics; shared resource defense against lions or alien hyenas promotes subgroup fusion, and intense resource competition generally limits subgroup size and promotes subgroup fission (Smith et al. 2008). In contrast to many gregarious species in which subgroups are more stable

and decisions regarding movement are made communally (Conradt & Roper 2005), spotted hyenas generally make individual decisions to join and leave subgroups (Gittleman 1989). In this system, individuals can vary in their propensity to socialize and act in their best interest in terms of social behavior (Smith et al. 2008). Studies have examined partner choice in hyenas to determine whether there are advantages to socializing with other group members. Smith et al. (2007) found that adult females most often associate with higher-ranking females and with those females occupying adjacent rank positions in the clan's dominance hierarchy. Both partners in these associations benefit; dominant hyenas benefit from priority of access to resources defended by a group, whereas subordinate hyenas receive reduced aggression from dominants at kills and better access to resources (Holekamp et al. 1997b; Boydston et al. 2001; Smith et al. 2007).

Hyenas frequently engage in several types of affiliative behaviors, including greeting behavior, in which two or more hyenas stand parallel to one another and reciprocally sniff the other's anogenital region (Kruuk 1972; East et al. 1993; Smith et al. 2011). These greeting ceremonies function either in the context of aggression to reconcile opponents and prevent escalation (Wahaj et al. 2001), or as nonconciliatory greetings unrelated to aggression (East et al. 1993; Colmenares et al. 2000). Smith et al. (2011) tested three hypotheses regarding nonconciliatory greeting behavior in hyenas and found that these greetings function to reinforce affiliative relationships, rather than to reduce social tension or to signal submission. Hyenas tended to solicit more greetings from preferred companions and greet more often with high-than low-ranking hyenas; greetings also offer opportunities for hyenas to assess the cooperative potential of a partner (Smith et al. 2011). There is limited evidence for inter-

individual variation in greeting behavior in hyenas; Smith et al. (2011) found that individuals are consistent across observations in the duration of their greetings.

In light of the advantages of associating with conspecifics, sociability may provide considerable benefits to hyenas in terms of fitness. Hyenas face intense feeding competition, because they feed in large groups on ephemeral kills. An individual can eat as much as 15kg of food in 15 minutes, and a group of hyenas can consume an entire carcass in that amount of time (Kruuk 1972; Holekamp & Smale 1996). Because food is a limited resource and the reproductive success of female hyenas is strongly driven by access to resources (Holekamp & Smale 1996), gaining feeding tolerance via associations with conspecifics might represent a significant fitness advantage for females.

In this chapter, we first assess the situational factors promoting sociability among hyenas, then determine whether there is evidence of consistent differences in sociability among individuals. We assess the stability of sociability across ontogeny, and determine whether genetics and maternal effects are responsible for inter-individual variation in sociability. Finally, we investigate the relationships between sociability and reproductive success and longevity.

METHODS

Study Subjects

Between 1988 and 2009, personnel from the Mara Hyena Project collected behavioral data on a group of free-living spotted hyenas, called the Talek Clan, in the Masai Mara National Reserve, Kenya (Boydston et al. 2001). All hyenas in this clan were recognized individually by

observers based on their unique spot patterns, and were of known sex, age, and social rank. Hyenas were sexed based on the morphology of the glans of the erect phallus (Frank et al. 1990). We assigned ages to all natal animals (to ± 7 days) based on their appearance when they were first seen above ground at dens, and we were able to assign immigrant males' ages reliably (to ± 6 months) with an age-estimation model (Van Horn et al. 2003).

The social rank of each hyena in the clan was assigned using a dominance matrix based on observations of dyadic agonistic interactions (Holekamp & Smale 1993; Smale et al. 1993). Rank was reassessed each time a new animal reached adulthood, entered or left the clan, or died. Cubs were assigned the rank of their mother until they reached reproductive maturity at 24 months of age (Frank 1986; Glickman et al. 1992; Holekamp et al. 1997a). We calculated standardized rank for each hyena by dividing their numerical rank by the total number of ranked animals in the clan at the time.

We established maternity based on genotyping and observations of cubs nursing (Holekamp & Smale 1993). Paternity was assigned based exclusively on genotyping, as previously described (Van Horn et al. 2004; Watts et al. 2011). Methods used to immobilize animals and collect blood samples for DNA extraction are described in detail in Engh et al. (2002). All sampling procedures were approved by the Institutional Animal Care and Use Committee at Michigan State University (AUF 07/08-099-00), complied with Kenyan law, and conformed to guidelines approved by the American Society of Mammalogists (Sikes & Gannon 2011).

Data collection

We generally observed hyenas from vehicles daily between 0530 and 0930 hours and between 1700 and 2000 hours. We initiated observation sessions whenever we saw a hyena or group of hyenas separated from conspecifics by at least 200 meters. Upon initiating an observation session, we recorded the GPS location of the session and conducted a behavioral scan that identified each hyena, noted its current behavior, and described its position in space relative to landmarks and conspecifics; these scans were repeated every 20 minutes. During each session, we used critical incident sampling (Altmann 1974) to record all occurrences of specific behaviors including aggressive acts, appeasements, vocalizations, and greetings. We also recorded whenever a hyena entered or left a session in progress.

In this study, we used four measures to describe the sociability of each individual: (1) its tendency to solicit greetings, (2) its greeting count, (3) its lifetime greeting rate, and (4) its mean group joining rate. First, during each observation session where an individual was present with at least one other hyena, we determined whether or not the hyena solicited at least one greeting. “Soliciting” a greeting involved a hyena lifting its leg to initiate a greeting with another hyena. We also calculated the number of greetings a hyena solicited during each observation session where at least one other hyena was present; this was called the greeting count for the hyena in that session. Following Van Meter (2009) and Smith et al. (2011), we calculated hourly adjusted greeting rates for each individual present in each session as:

$$\frac{\text{number of greetings solicited} \div \text{number of potential greeting partners}}{\text{number of hours the session lasted}}$$

where the number of potential greeting partners was a count of all other hyenas present in the observation session. This measure controlled for variation in the number of opportunities each hyena had to solicit greetings during each session. To calculate a lifetime greeting rate for each hyena, we averaged its greeting rates in all its sessions with conspecifics after it reached 24 months of age. For our final measure of sociability, we calculated the hourly rate at which each hyena joined other groups of hyenas during the period between 1996 and 2002. A hyena was determined to have joined another group if it approached and remained within 200 meters of at least one other hyena. To calculate the hourly group joining rate, we divided the number of joining events for each individual during the seven-year period by the number of hours that the individual was observed during this period.

Other situational data were also collected from all observation sessions, including the maximum number of hyenas present in the session, the time of day (either from midnight to noon, or from noon until midnight), the location of the session (at a communal den, a kill, a carcass, a mating event, a natal den, or a session away from these contexts), and the current seasonal prey availability (high for June to October, and low from November to May).

Statistical Analysis

Bayesian analyses

For many of our analyses, we adopted a Bayesian approach and created models with the Markov Chain Monte Carlo for Generalized Linear Mixed Models (MCMCglmm) analysis tool in the R statistical package (Hadfield 2010; R Core Development Team 2011). For each of these analyses, we tested fixed effects for significance by determining whether or not the 95%

credible interval for the fixed effect included zero; variables for which the credible interval included zero were not significant predictors of the response variable, whereas those that did not include zero were considered significant. We tested random effects for significance by comparing the deviance information criterion (DIC) values of models fitted with and without the random effect of interest; if the inclusion of a random effect lowered the DIC value of the model, the random effect was considered significant in predicting the response variable.

For zero-inflated MCMCglmm models, we began by using a saturated model with fixed effects contributing to both the poisson and zero-inflated portions of the model, but we only retained zero-inflation terms that lowered the DIC value of the model. In the zero-inflated portion of the model, the estimates for fixed effects were interpreted as the $\log(e)$ of the ratio of the odds of the response variable not occurring, compared to the odds of the response variable occurring.

For all MCMCglmm models, we used a relatively uninformative prior that partitioned variance equally among all random effects (Hadfield 2010); using a more informative prior did not affect reported results. Estimates are reported as posterior means with 95% credible intervals. We assessed convergence of these models by examining time series of the model parameters. We also inspected autocorrelation values for these models, all of which were less than 0.1 for reported values.

Situational factors influencing sociability

We assessed sociability based on two different levels of analysis; one at the level of the observation session, and another at the level of individual hyenas. First, we performed an

analysis using the observation session as the unit of analysis to determine which social and environmental factors influenced how often hyenas greeted.

As the response variable for this analysis, we summed the greeting count in each observation session for all adult hyenas present; this measure represented a general measure of sociability for each observation session. Using this composite measure of sociability allowed us to assess the importance of situational variables that were common to all hyenas present in the session. We fitted a MCMCglmm model with the total greeting count in each observation session as the response variable, and various social and environmental aspects of the session as fixed effects. These fixed effects included the location of the session, the duration of the session, the time of day, the maximum number of hyenas present in the session, and whether seasonal prey availability was high or low.

Consistency in sociability within individuals

We then performed a similar Bayesian analysis using individual hyenas as the units of analysis to (1) determine which characteristics of individuals affected sociability, and (2) determine whether there was within-individual consistency over time in this measure of sociability.

In the individual-level analysis, we used the greeting count of each hyena in each session as the measure of sociability. For each sex, we created a separate repeated measures MCMCglmm model with the greeting count of each adult hyena in each session as the response variable. The standardized social rank and age of the hyena on the date of the session were included as fixed effects. A unique session identifier was included as a random effect in each

analysis to control for pseudoreplication. To determine whether individual hyenas were consistent in the frequency of greets they solicited across observation sessions, we tested whether the inclusion of a random effect representing the identity of the hyena improved each model. If this term significantly improved the fit of these models, individuals' behavior could be considered consistent across repeated observations. Only hyenas present during adulthood in at least 20 observation sessions with potential greeting partners in were included in this analysis.

Heritability of sociability

To determine whether or not sociability is heritable in spotted hyenas, we created restricted-likelihood Bayesian animal models (Kruuk 2004). Animal models use pedigree information to partition the heritable and non-heritable components of phenotypic variance (Kruuk 2004; Wilson et al. 2009). Phenotypic, additive genetic, and maternal effects were estimated with univariate-trait animal models predicting the sociability of each hyena. Because female hyenas mate with several males across their reproductive history, maternal effects can be distinguished from heritability via the effect of these different sires.

As the response variable of our first animal model, we used the lifetime greeting rate of each hyena. Only hyenas that were present with potential greeting partners in at least 50 sessions after 24 months of age were included in this analysis.

We included sex and average lifetime standardized rank as fixed effects, but only retained fixed effects that contributed significantly to the model. We included random effects representing the additive genetic effect and the identity of the hyena's mother. We calculated

heritability and maternal effects by dividing the relevant variance component by the total phenotypic variance.

Because MCMCglmm requires values for all random effects, we generated unique maternal identities for immigrant males and natal animals born before our study began, following Taylor et al. (2012). This technique allows for the estimation of maternal effects, even when pedigree information is missing; however, it assumes that all hyenas with unknown maternity are unrelated.

We also created and ran an animal model that was identical to the one described above, except that here we used the group joining rate of each hyena as the response variable. Heritability and maternal effects were calculated as described above. Only hyenas that were observed for at least 15 hours between 1996 and 2002 were included in this analysis.

Stability over time and across situations

In order to determine whether the sociability of individual hyenas remained stable across ontogeny, we created generalized linear mixed models using the lme4 function in R. We determined the tendency to greet in each session for all cubs less than 8 months of age, as well as the tendency to greet in each session for hyenas that were at least 24 months of age. These data were used as the response variables in linear models involving repeated measures. Only female hyenas present with potential greeting partners in at least 50 sessions during each age class were included in this analysis.

We included age class (either cub or adult) as the main fixed effect of interest and included the hyena's standardized rank as a fixed effect. A unique session identifier was included as a random effect to control for pseudoreplication.

We included individual identity as a random intercept to allow for the variation among hyenas in greeting behavior that had been suggested by earlier analyses. We also added a random slope to the model, which described the extent to which the sociability of individual hyenas changed across ontogeny. If this term significantly improved the fit of the model, we could conclude that the sociability of individual hyenas did not change consistently across age classes. To test whether the random slope significantly improved the fit of the model, we created two models that were identical except for the inclusion of the random slope. We then compared these two models with a log-likelihood ratio test, in which the log-likelihood ratio is calculated as $2[\log\text{-likelihood of model B} - \log\text{-likelihood of model A}]$, and tested as a chi-squared distribution (Pinheiro & Bates 2000; Martin & Réale 2008). Finally, we included an interaction term between standardized rank and the random slope, to determine whether social rank determined how the sociability of individuals changed across ontogeny. Using a log-likelihood ratio test, we determined whether the inclusion of this interaction term significantly improved the fit of the model. The approach of using random regression to investigate behavioral reaction norms is described in more detail in Dingemanse et al. (2010).

Relationship between sociability and fitness

Finally we tested whether a hyena's sociability affected its fitness, as indicated by various measures of reproductive success and longevity. We used the lifetime greeting rate

and the overall group joining rate of each female as the measures of sociability in this analysis. For the greeting rate analysis, we only included females present during adulthood with potential greeting partners in at least 50 sessions. For the joining rate analysis, we only included adult females that were observed for at least 15 hours between 1996 and 2002.

As indicators of reproductive success, we used the total number of cubs borne by each female over her lifetime, as well as the proportion of her cubs that survived to three life-history milestones: den independence, weaning, and 24 months of age. We created a set of generalized linear and second-order polynomial models with these fitness components as the response variables, and the sociability measure of interest, the maternal rank of the female, and an interaction term as predictors. Separate analyses were carried out for greeting rate and group joining rate. Only female hyenas that were born after our study began and died before our study ended were included in these reproductive success analyses.

We also used hyenas' longevity as a response variable to determine whether sociability is related to survival. For this dataset, we used the same two measures of sociability and criteria for inclusion, except we included only females for which we had known death dates. We created both generalized linear and second-order polynomials with longevity (in months) as the response variable. As fixed effects, we included the sociability measure of interest and the average lifetime standardized rank of the female, as well as an interaction term between these variables. Separate analyses were run for greeting rate and group joining rate.

For longevity and all measures of reproductive success, we used likelihood ratio tests to determine whether second-order polynomial models were able to predict these fitness measures better than linear models. All variables in these analyses were Z-transformed.

RESULTS

Social and environmental factors influencing sociability

Between 1988 and 2009, there were 10526 observation sessions that met our criteria for inclusion in the analysis of greeting count. In 8775 (83.4%) of these sessions, hyenas did not greet at all. Greetings were less common at kills than at sessions away from dens, mating, and food, and hyenas solicited a greater number of greetings between noon and midnight than between midnight and noon (Appendix, Table 4.A1). Hyenas solicited more greetings in sessions with longer durations and in sessions with more hyenas present than in shorter sessions or those with fewer hyenas present (Appendix, Table 4.A1).

Consistency in sociability within individuals

Eighty-five females met our criteria for this analysis. Older females were less likely than younger females to solicit greetings in a session, and there was a non-significant trend for lower-ranking hyenas to solicit more greetings than did higher-ranking hyenas (Appendix, Table 4.A2). Ninety-six male hyenas met our criteria for this analysis. Both standardized rank and age affected the number of greetings solicited by male hyenas; higher-ranking males solicited more greetings than did lower-ranking males, and older males solicited more greetings than did younger males (Appendix, Table 4.A3).

For members of both sexes, the inclusion of a random effect of individual improved the fit of the model (Table 4.1), suggesting that both males and females were consistent over time with respect to the frequency at which they solicited greetings.

Table 4.1

DIC values yielded by MCMCglmm models predicting the number of greetings solicited in each observation session by adult (≥ 24 months of age) female and male hyenas. DIC values are given for models with only a random effect of the session identifier, and for models run with both a session identifier and an individual identifier. For each sex, the better model is marked with an asterisk.

Sex	Random effects included	
	Session	Individual and Session
Females	17789.79	15606.06*
Males	5456.81	4615.105*

Heritability of sociability

For lifetime greeting rate, genetic and maternal effects were both significant, as indicated by a lower DIC value when these effects were included (-863.521), compared to when they were omitted (genetic effect omitted, DIC=-834.117; maternal effect omitted, DIC=-848.817). The heritability estimate from the MCMCglmm animal model for lifetime greeting rate was 0.160 (95% CI=0.0305 to 0.605, Figure 4.1) and the maternal effect estimate was 0.068 (95%CI=0.026 to 0.312, Figure 4.1).

For group joining rate, genetic and maternal effects were both significant, as indicated by a lower DIC value when these effects were included (131.586), compared to when they were omitted (genetic effect omitted, DIC=139.349; maternal effect omitted, DIC= 136.554). The heritability estimate from the MCMCglmm animal model for the group joining rate was 0.090 (95% CI=0.024 to 0.397, Figure 4.1) and the maternal effect estimate was 0.088 (95%CI=0.024 to 0.336, Figure 4.1).

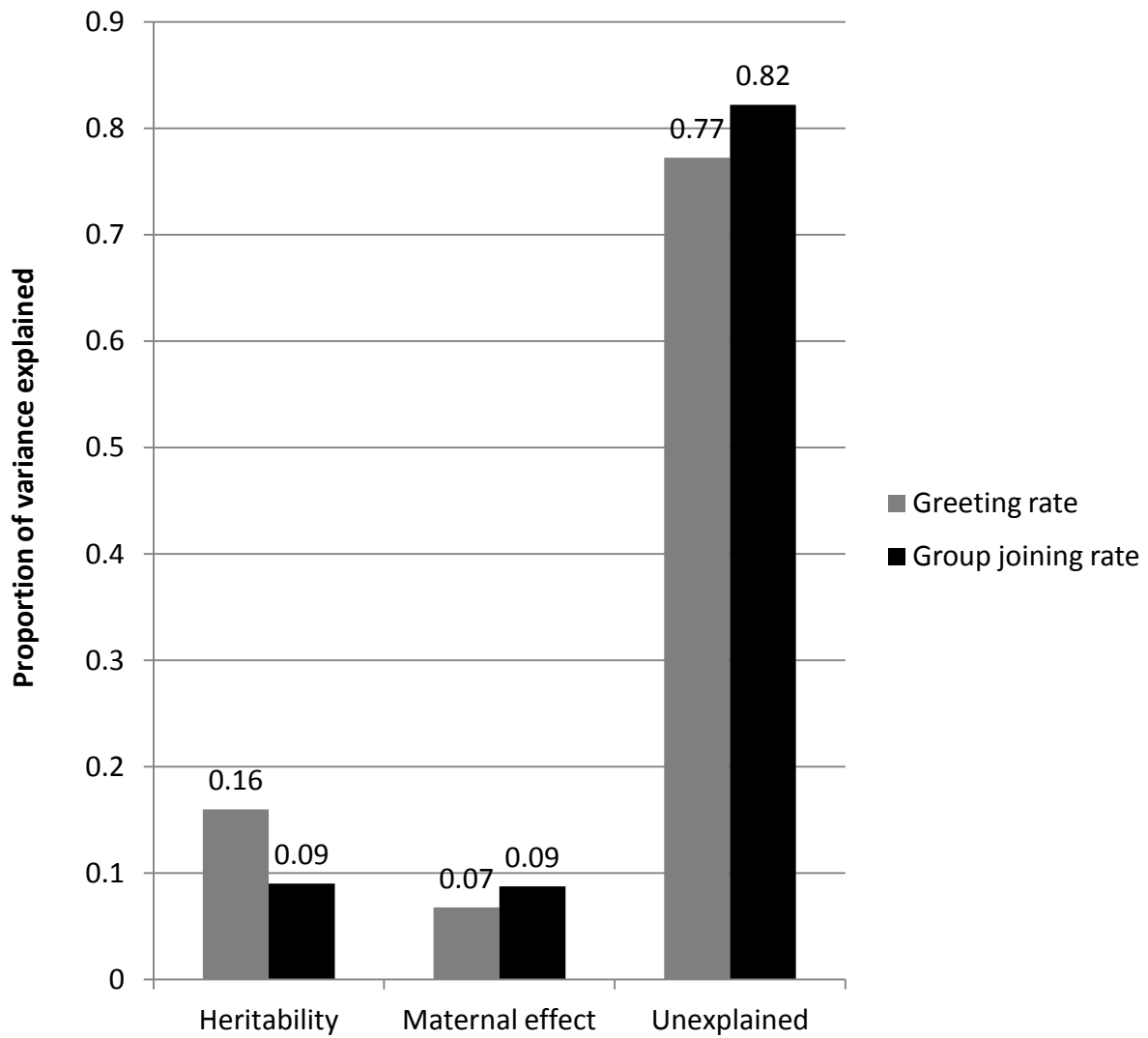


Figure 4.1. For two measures of sociability, the percent of variation attributable to heritability, maternal effects, and the remaining unexplained variation. Variances were estimated with separate MCMCglmm animal models.

Stability of sociability

There were 42 female hyenas with potential greeting opportunities in at least 50 sessions during each of the two age classes. The model that included a random slope of age class in addition to the random intercept was significantly better at predicting the likelihood of greeting in a session than the model with only the random intercept (LRT=58.680, df=2, $p<0.001$), indicating that within individuals, sociability does not change in consistent ways across ontogeny (Figure 4.2).

The model that included an interaction between standardized rank and the random slope was significantly better at predicting the data than the random slope model without this interaction term (LRT=15.417, df=7, $p=0.031$), indicating that social rank affected how sociability changed across ontogeny. The interaction was positive (29.625 ± 5.443), suggesting that as social rank decreased, females became more likely to greet as adults, compared to when they were cubs.

Relationship between sociability and fitness

Thirty-eight females satisfied the criteria for inclusion in our analysis of the relationship between greeting rate and reproductive success. Using generalized linear models, lifetime greeting rate was not a significant predictor of any measure of reproductive success as a fixed effect or in an interaction with maternal rank ($p>0.1$). Second-order polynomial models failed to describe the data better than linear models ($p>0.1$)

There were 31 females that satisfied the criteria for inclusion in our analysis of the relationship between group joining rate and reproductive success. In generalized mixed

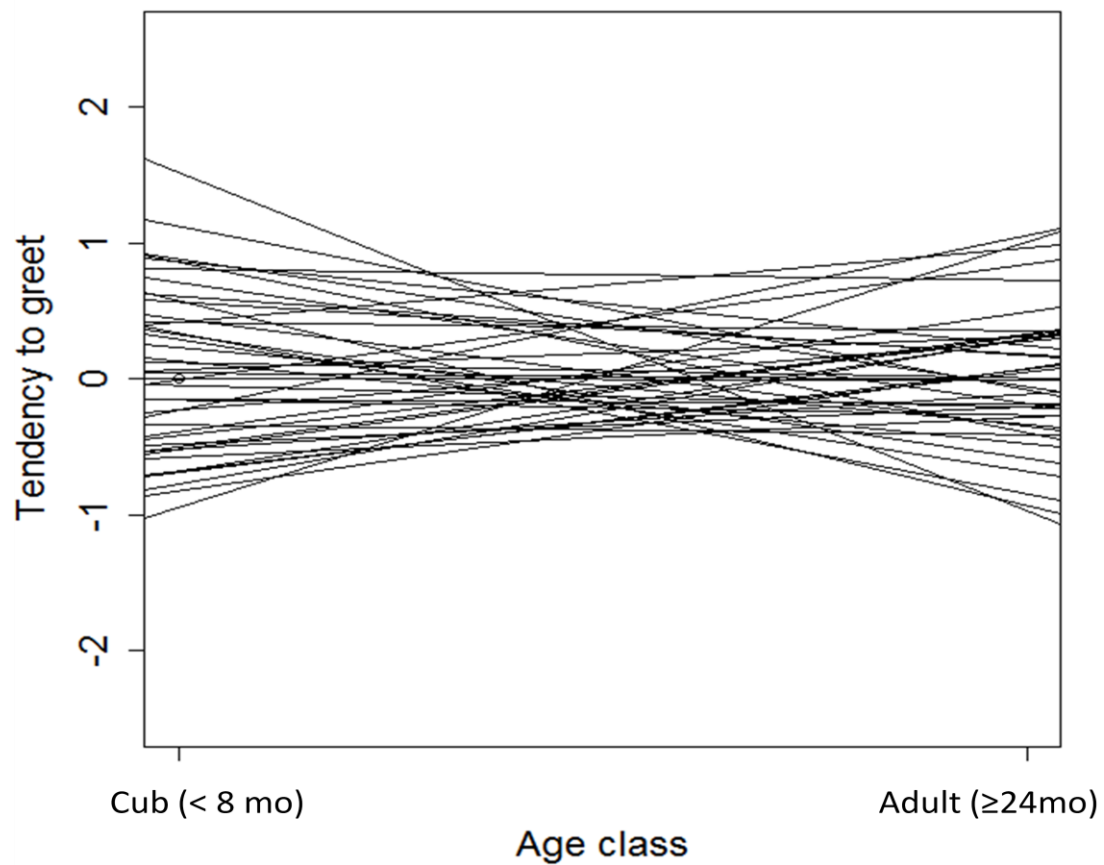


Figure 4.2. Predicted behavioral reaction norms for the likelihood of greeting across two age classes, as predicted by lmer models. Each line represents how the behavior of a female changes across ontogeny. Smaller likelihoods of greeting represent less sociable individuals, as these individuals are less likely to greet with other hyenas in a session.

models, group joining rate was not significant in predicting any measure of reproductive success. However, we found several significant interactions between group joining rate and maternal rank. Although high-ranking hyenas had consistently high reproductive success, low-ranking females with high group joining rates enjoyed better reproductive success than did low-ranking females with low group joining rates. The interaction between maternal rank and group joining rate was significant for all measures of reproductive success associated with offspring survivorship, including the percent of cubs surviving to weaning (0.022 ± 0.007 , $t=3.292$, $p=0.003$), the percent of cubs surviving to den independence (0.024 ± 0.007 , $t=3.447$, $p=0.002$), and the percent of cubs surviving to reproductive maturity (0.018 ± 0.007 , $t=2.615$, $p=0.014$).

There were 64 female hyenas that satisfied the criteria for inclusion in our analysis of the relationship between greeting rate and longevity. The age at death of these females averaged 108.80 ± 5.77 months. Greeting rate was not significantly related to longevity, using either generalized linear or second-degree polynomial models ($p>0.1$). Furthermore, no interaction terms containing greeting rate significantly predicted longevity ($p>0.1$).

There were 34 female hyenas that satisfied the criteria for inclusion in our analysis of the relationship between group joining rate and longevity. The age at death of these females averaged 112.38 ± 1.30 months. Group joining rate significantly predicted age at death; hyenas that joined groups more often lived longer than did those that joined groups less often (19.820 ± 7.354 , $t=2.695$, $p=0.011$, Figure 4.3). No interaction terms containing group joining rate significantly predicted longevity, and second-order polynomial terms were not significantly better than linear models at predicting age at death ($p>0.1$).

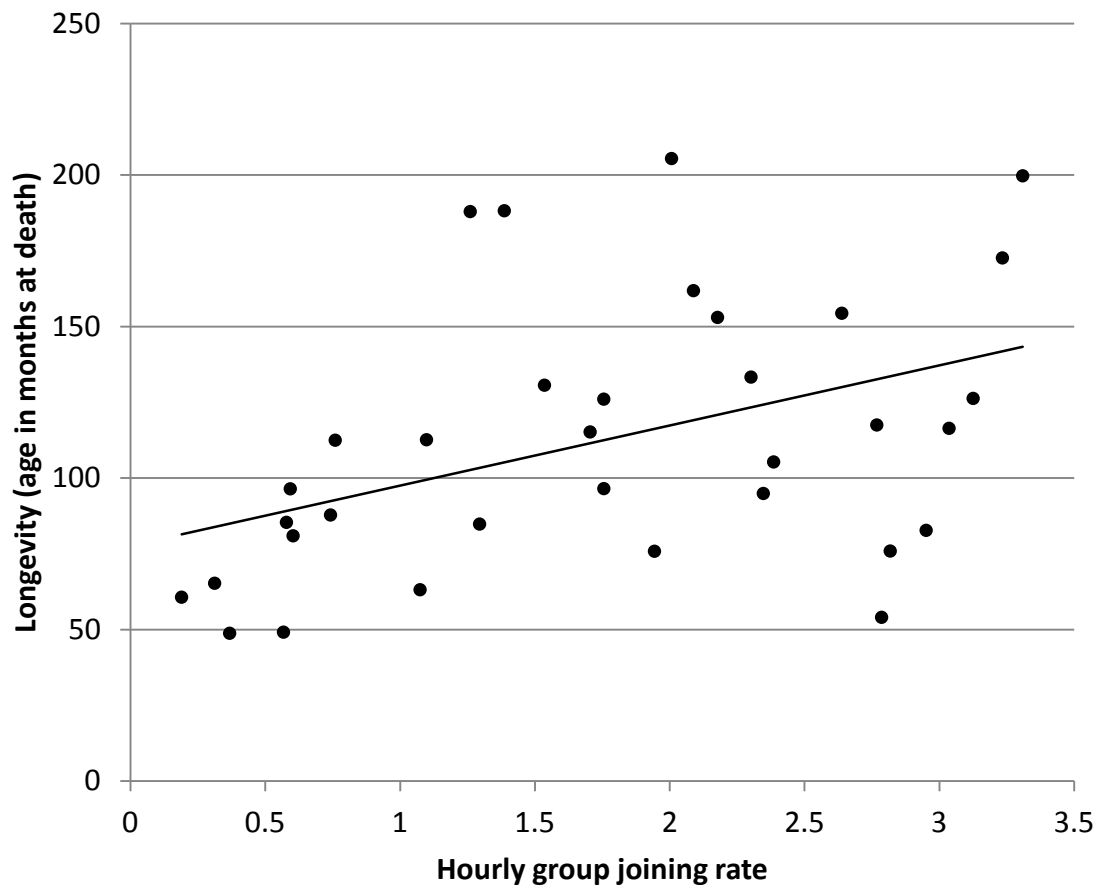


Figure 4.3. The relationship between group joining rate and longevity. Group joining rate was calculated as the hourly rate at which adult females joined groups between 1996 and 2002. Actual values are displayed as dots, and the values predicted by generalized linear model are shown as a line.

DISCUSSION

Both situational factors and individual attributes at the time of the session affected the number of greetings solicited by hyenas. Hyenas solicited fewer nonconciliatory greetings at kills than in other situations; in other words, these greetings occurred less frequently in situations where tension was high due to resource competition than they did in situations with less tension. This supports previous research showing that nonconciliatory greetings do not function to reduce social tension (Smith et al. 2011). Interestingly, there was a non-significant trend for hyenas to solicit a greater number of greetings when seasonal prey abundance was low. Social relationships may be especially important to maintain when resource availability is reduced, due to the increased importance of feeding tolerance during these periods.

High-ranking males solicited more greetings than low-ranking males. This effect may be due to our inclusion of both immigrant and adult natal males in this analysis; adult natal males outrank immigrant males, and may be more likely to greet with members of their natal clan than immigrants are. The relationship between rank and greeting behavior was reversed in females; we observed a non-significant trend for low-ranking females to solicit more greetings than higher-ranking females. Adult females prefer to solicit greetings from higher-ranking individuals (Smith et al. 2011), and low-ranking females have a larger number of dominant animals with which to forge bonds than do higher-ranking females.

Our results show that adult hyenas were consistent across repeated observations in the number of greetings they solicited; we found significant inter-individual differences in this measure of sociability for both males and females. From our heritability analyses, we estimated that about 16 percent of the observed phenotypic variation in the frequency with

which hyenas solicit greetings was due to genetic effects, and for the rate at which hyenas join groups, about 9 percent of the observed phenotypic variation was due to genetic effects. These heritability estimates are significantly smaller than those reported for sociability in humans (e.g. Plomin 1994), and are also lower than the average heritability estimate for behavioral traits in non-human animals, which is 0.30 ± 0.02 (Mousseau & Roff 1987). However, they show that genetics play a significant role in shaping sociability, and that sociability is more strongly heritable than some other traits in hyenas, such as boldness (see Chapter Two). As noted previously, differences between heritability and maternal effect estimates were due to sire effects within dams. Despite significant heritability and maternal effect estimates, a large amount of the phenotypic variance observed in both greeting behavior and group joining behavior remained unexplained by our models. One potential explanation for this unexplained variation is the effect of early experience on sociability. There is accumulating evidence that experience is important in determining sociability in non-human primates; periods of maternal separation and reduced maternal care have been found to reduce social tendencies in pigtail macaques (Caine et al. 1983; Capitanio & Reite 1984), and Andrews and Rosenblum (1991) found that fluctuating resource availability early in life affected social competence in bonnet macaques. Hyenas show many similarities to cercopithecine primates in terms of both social structure and cognition (Drea & Frank 2003; Holekamp et al. 2006), and thus it is likely that early experience contributes to some of the inter-individual variation in sociability observed in hyenas, as it does in highly social primates.

Interestingly, sociability does not appear to be stable across ontogeny; individuals that are particularly likely to solicit greetings as cubs are not generally more likely to solicit greetings

as adults. This runs contrary to our findings regarding aggressiveness and boldness in hyenas, each of which appear to be determined relatively early in life (see Chapters Two and Three). This effect may be partially explained by our finding that as social rank decreases, the tendency to greet increases across ontogeny. In other words, low-ranking individuals are more likely than high-ranking individuals to solicit more greetings as adults than they did as cubs. Before they are 8 months old, cubs are still learning their social ranks in relation to those of their peers, and do not yet understand their social rank in relation to older hyenas (Holekamp & Smale 1993; Smale et al. 1993); therefore, rank likely has little or no effect on greeting behavior during this time. However, after reaching reproductive maturity, social rank potentially has large ramifications for greeting behavior. As discussed previously, there are more dominant greeting partners available to females of low social status than to those of high social status. Furthermore, limited access to resources may drive lower-ranking females to seek out the advantages conferred by greeting, such as reinforced social bonds with cooperative and affiliative partners, especially those of high rank (Smith et al. 2011).

In a similar vein, we found that the strength of the relationship between sociability and reproductive success depended on social rank. Whereas high-ranking females tended to enjoy high offspring survivorship no matter how social they were, the offspring of lower-ranking females that joined groups more often were more likely to survive to den independence, weaning, and reproductive maturity than were the offspring of lower-ranking females that did not join groups as often. This indicates that the benefits of sociability are particularly large for lower-ranking hyenas. Previous studies have shown that by associating with higher-ranking females, subordinate females gain reduced aggression at kills and better access to resources

(Holekamp et al. 1997b; Boydston et al. 2001; Smith et al. 2007); these advantages likely translate to an increase in feeding time for hyenas that are particularly social. Because the reproductive success of female hyenas is strongly driven by access to resources (Holekamp & Smale 1996), better access to food may be responsible for the increased survival of the offspring of more gregarious low-ranking females, compared to low-ranking females that are less social. It is interesting that both sociability and aggression (see Chapter Three) have more significant ramifications for the reproductive success of low- than high-ranking hyenas. For species such as hyenas, in which access to resources is vastly different for dominant and subordinate individuals, the consequences of personality traits that affect resource holding power may have especially large effects on low-ranking individuals. Findings regarding this phenomenon are inconsistent; in contrast to our findings, the benefits of sociability are independent of dominance in baboons, a species with a similar rank-based social organization (Silk et al. 2003). The interaction of personality, social rank, and fitness may depend on many factors, such as rigidity of the dominance hierarchy, the availability of food, and the benefits (or disadvantages) conferred by the personality trait.

The lifespan of adult female hyenas was positively correlated with the rate at which they joined subgroups within their fission-fusion society. This resembles earlier results from baboons, in which females with more social support tended to live longer than those with less social support (Silk et al. 2010). We know that there are definite benefits associated with social behavior in both hyenas and baboons (Silk et al. 2006; Smith et al. 2007; Smith et al. 2010), but it is not yet clear exactly how sociability affects longevity in hyenas. Although starvation is not a major source of mortality among spotted hyenas (Kruuk 1972; Watts & Holekamp 2009),

increased access to resources may play an indirect role in prolonging lifespan. Moreover, because sociability reinforces bonds and promotes cooperation (Smith et al. 2011), hyenas that frequently engage in social behavior may have more allies present and thus enjoy better protection during attacks from lions or neighboring groups of hyenas.

Future researchers should strive to elucidate the mechanism by which sociability is related to survival in hyenas, as this remains poorly understood. Additionally, because we were only able to explain less than a quarter of the phenotypic variation in the greeting solicitation rate and group joining rate of hyenas, it would be fruitful to determine what other factors contribute to inter-individual variation in sociability in this species. Neuropeptides, oxytocin, and other hormones are known to influence social behavior in other species (Fries et al. 2005; Lim & Young 2006), but whether hormonal mediation of sociability occurs in hyenas is currently unknown. Other studies suggest that resource availability or periods of reduced maternal care may affect sociability via early experience (Capitanio & Reite 1984; Andrews & Rosenblum 1991). It is also possible that litter or cohort effects may play a role in sociability in hyenas, as these have been found to shape personality traits in other species (e.g. Taylor et al. 2012). Finally, it would be particularly interesting to study the ramifications of sociability, as well as other personality traits, in other species where access to resources is extremely unequal. This type of study would help clarify the circumstances in which personality and social rank interact to affect the fitness of dominant and subordinate animals in different ways.

APPENDIX

Table 4.A1

Situational variables predicting the average greeting count in each observation session.

	Posterior mode	(95% credible interval)	p _{MCMC}
<i>Poisson</i>			
(Intercept)	-2.49937	(-3.27394 to -0.6501)	<0.002*
Location (carcass)	0.19204	(-0.19259 to 0.50616)	0.32
Location (den)	0.0752	(-0.12020 to 0.27166)	0.456
Location (kill)	-0.41461	(-0.65320 to -0.10078)	0.004*
Location (mating event)	0.37107	(-0.01014 to 0.78210)	0.052
Location (natal den)	0.08447	(-0.32860 to 0.43825)	0.68
Time of day (PM)	0.52476	(0.11271 to 0.75499)	<0.002*
Number of hyenas present	0.10805	(0.05401 to 0.13304)	<0.002*
Session length	0.25974	(0.12581 to 0.42382)	<0.002*
Prey availability (low)	0.1246	(-0.01150 to 0.29387)	0.076
<i>Zero-inflated</i>			
(Intercept)	2.50302	(2.03461 to 2.85827)	<0.002*
Session length	-3.27528	(-3.83302 to -2.26259)	<0.002*

Table 4.A2

Fixed effects predicting the number of greetings solicited by each adult (> 24 months of age) female hyena in each observation session.

	Posterior mode	95% credible interval	p _{MCMC}
<i>Poisson</i>			
(Intercept)	-2.552586	(-2.996015 to -1.882476)	0.003*
Age	-0.001007	(-0.003943 to 0.001459)	0.4686
Standardized rank	0.960474	(-0.066043 to 2.014638)	0.0743
<i>Zero-inflated</i>			
(Intercept)	-0.107573	(-0.640567 to 0.578720)	0.5943
Age	0.012174	(0.008033 to 0.015028)	<0.003*
Standardized rank	-0.31696	(-1.254729 to 0.592191)	0.601

Table 4.A3

Fixed effects predicting the number of greetings solicited by each adult (> 24 months of age) male hyena in each observation session.

	Posterior mode	95% credible interval	p _{MCMC}
<i>Poisson</i>			
(Intercept)	-2.012691	(-2.76507 to -1.318199)	<0.003*
Age	0.008833	(0.002756 to 0.016745)	<0.003*
Standardized rank	-1.722163	(-2.905801 to -0.046431)	0.041*
<i>Zero-inflated</i>			
(Intercept)	1.123227	(0.331993 to 1.816341)	<0.003*
Age	-0.019016	(-0.029105 to -0.010240)	<0.003*
Standardized rank	-2.071601	(-3.530891 to 0.432572)	0.137

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LITERATURE CITED

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